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# A CONTRIBUTION TO THE POLLEN MORPHOLOGY OF NEOTROPICAL LAURACEAE<sup>1</sup>

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## ABSTRACT

The present study is a pollen-morphological investigation of 80 species belonging to 17 of the 22 known neotropical genera of Lauraceae. Observations were made with light and scanning electron microscopes. An ultrastructural study of the pollen wall of 11 genera was also undertaken by transmission electron microscopy. The pollen grains of most of the genera are easily identifiable by their sizes and by the number and organization of spinules. The pollen grains of all the species investigated are apolar, spheroidal, and inaperturate. The exine is very thin and coherent due to loosely or densely packed globular to variously shaped bodies. The surface of exine is scattered with pointed or blunt, monomorphic or dimorphic spinules. The spinules are made up of numerous tightly woven strands; their bases are encompassed by a thick, circular, cushionlike form. The intine was found to be the dominant layer of the pollen wall and to show varied composition and structural details. It is remarkable that a similar type of intine has been encountered in the inaperturate pollen grains belonging to such disparate genera as *Canna*, *Heliconia*, *Hernandia*, and *Palmeria*. The taxonomic implications of the palynological observations are discussed.

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## TAXONOMIC REVIEW AND CLASSIFICATION

Lauraceae form a large, predominantly tropical family of trees and shrubs. The sole exception is the genus *Cassytha*, which consists of leafless, twining parasites much like *Cuscuta* (Convolvulaceae). *Cassytha* is sometimes treated as a separate family, but since it differs only in habit from the woody Lauraceae, we maintain it in the Lauraceae. Centers of species richness are tropical Asia and tropical America. Lauraceae are rather poorly represented in Africa, are rather diverse in Madagascar, and occur in Australian rain forests, the Pacific Islands, and in New Zealand (two species).

The family is easily recognized by its flow-

ers. The perianth consists of two cycles of three tepals each, which are usually equal. By far the most common flower colors vary from white to green or yellowish; very rarely does one encounter reddish flowers (*Kubitzkia*). The stamens are also arranged in cycles of three each, and in principle there are four staminal cycles. The fourth or innermost cycle is nearly always reduced to staminodes or is entirely lacking. Three cycles are usually present but can be reduced to two or one fertile cycle in some genera. The three stamens of cycle three have nearly always two glands attached at or near their base. In the genus *Pleurothyrium* these glands become greatly enlarged and surround all nine fertile

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stamens. The ovary is superior (except in the monotypic African *Hypodaphnis*), has one locule, and develops into a drupe, which may be subtended by the enlarged floral tube. The flowers can be perfect or unisexual.

Although the Hernandiaceae and Monimiaceae are frequently mentioned as close relatives of the Lauraceae, flowers of Lauraceae are rarely confused with other families.

The Lauraceae are of considerable economic importance. *Persea americana* is widely cultivated for its edible fruit, the avocado. Most species of Lauraceae possess varying amounts of aromatic oils, some of which are economically important. Examples are camphor oil from *Cinnamomum camphora*; rosewood oil from *Aniba rosaeodora*; and Brazilian sassafras oil from *Ocotea odorifera*.

The bark of *Cinnamomum verum* yields cinnamon. Leaves of *Laurus nobilis* and *Umbellularia californica* are used as spices (bay leaves); in Central America, *Litsea glaucescens* is used for the same purpose. Several other species are used on a local basis, for instance *Sassafras albidum* for the preparation of root beer and *Dicypellium caryophyllatum* (now supposedly very rare due to excessive exploitation) for its spicy fruits. The wood of many species of Lauraceae is valuable. Some species have unusually hard or decay-resistant wood used for construction, and the wood of other species is excellent for making furniture (Richter, 1981).

#### CLASSIFICATION

A workable generic classification of the Lauraceae does not yet exist. Several reasons lie behind the poor understanding at generic level. The most important reason is that, with very few exceptions (*Cassytha*, *Hypodaphnis*), the genera do not have exclusive characters, that is, characters restricted to one particular genus. As a consequence, the genera are separated by combinations of characters. Very often both floral and fruit characters are used, and, because specimens only rarely have flowers and fruits (fruits usually

require one or two months to mature), keying specimens to genus is frequently impossible. A second difficulty is that in some cases the characters separating genera are weak or difficult to interpret. Thus, even perfect specimens cannot always be unambiguously assigned to a genus.

Results of these difficulties are that many generic identifications are suspect and that species are frequently transferred between genera or described in incorrect genera. It seems that the Lauraceae are the only family in which every botanist who seriously worked on the family has redescribed an already published species in a genus different from the one in which it was previously described.

Tables 1, 2, and 3 present three recent generic classifications of Lauraceae. Tables 1 and 2 are abbreviated versions of classifications by Kostermans (1957) and Hutchinson (1964) based on flower and fruit characters. Table 3 shows Richter's (1981) generic groupings and is based on studies of secondary xylem and bark. *Cassytha*, not being woody, is excluded from Richter's groupings.

Kostermans (1957) recognized five tribes in the woody Lauraceae, which are separated on inflorescence and cupule characters. One tribe consists solely of the African *Hypodaphnis*, which has an inferior ovary. The other four tribes occur in the New World. They are the Perseae (inflorescence exinvolucrate, cupule lacking), subdivided into two subtribes; the Cinnamomeae (inflorescence exinvolucrate, cupule present), likewise subdivided into two subtribes; the Litseae (inflorescence with decussate bracts, cupule present), subdivided into two subtribes; and the Cryptocaryeae (inflorescence exinvolucrate, drupe fully enclosed in floral tube), also subdivided. The subdivisions in each of these four tribes are based on numbers of anther cells.

Kostermans (1957) postulated an evolutionary trend in the Lauraceae from genera with a very shallow floral tube, where the fruit is not subtended by a cupule (tribe Perseae), through genera with a deeper floral tube, where the mature fruit is subtended by a cupule up to one-third the size of the fruit

TABLE 1. *Classification (after Kostermans, 1957) of the neotropical genera of Lauraceae.*

Subfamily Lauroideae	
Tribe	<b>Perseeae.</b> Inflorescence paniculate, exinvolucrate. Cupule absent.
Subtribe	Perseineae. Anthers four-celled.
Genera	<i>Persea</i> , <i>Phoebe</i> , <i>Caryodaphnopsis</i>
Subtribe	Beilschmiediineae. Anthers two-celled.
Genera	<i>Beilschmiedia</i> , <i>Mezilaurus</i>
Tribe	<b>Cinnamomeae.</b> Inflorescence paniculate, exinvolucrate. Cupule present.
Subtribe	Cinnamomineae. Anthers four-celled.
Genera	<i>Ocotea</i> , <i>Nectandra</i> , <i>Pleurothyrium</i> , <i>Sassafras</i> , <i>Umbellularia</i> , <i>Dicypellium</i>
Subtribe	Anibineae. Anthers two-celled.
Genera	<i>Aiouea</i> , <i>Aniba</i> , <i>Endlicheria</i> , <i>Licaria</i> , <i>Urbanodendron</i> , <i>Kubitzkia</i> , <i>Phyllostemonodaphne</i>
Tribe	<b>Litseeae.</b> Inflorescence involucrate with decussate bracts. Cupule present.
Subtribe	Litseineae. Anthers four-celled.
Genus	<i>Litsea</i>
Subtribe	Lauriineae. Anthers two-celled.
Genus	<i>Lindera</i>
Tribe	<b>Cryptocaryeae.</b> Inflorescence paniculate, exinvolucrate. Fruit fully enclosed in flower tube.
Subtribe	Eusideroxylineae. Anthers four-celled.
Genus	<i>Eusideroxylon</i> (not neotropical)
Subtribe	Cryptocaryineae. Anthers two-celled.
Genus	<i>Cryptocarya</i>
Tribe	<b>Hypodaphneae.</b> Ovary inferior.
Genus	<i>Hypodaphnis</i> (African)
Subfamily Cassythaideae	
Genus	<i>Cassytha</i>

(tribe Cinnamomeae), and through genera with a deep floral tube, where the fruit is fully enclosed in the floral tube (tribe Cryptocaryeae), to the tribe Hypodaphneae, where the fruit is fully enclosed in and becomes fused with the floral tube. This is a stimulating theory, although it is not certain whether it is phylogenetically accurate, that is, whether the Perseeae are indeed the most primitive tribe. The position of the Litseeae, recognized by their inflorescence type, is not clear in this theory.

Hutchinson (1964) also recognized five tribes of woody Lauraceae but defined his tribes quite differently. His Apollonieae are characterized by exinvolucrate inflorescence, two-celled anthers, and fruit not fully enclosed by floral tube. His Cryptocaryeae are as his Apollonieae except for the fruit being enclosed by the floral tube. Tribe III, the Sassafrideae, is of doubtful value; its single New World species, *Sassafridium veraguense*, has been placed by nearly all botanists during the last

century in *Ocotea*. This tribe is characterized by having all anthers with introrse cells. The Cinnamomeae (exinvolucrate inflorescence, at least one anther row extrorse, all anthers four-celled) differs from the Sassafrideae only in having some anthers extrorse. *Hypodaphnis* is placed in this tribe. The fifth tribe, the Litseeae, is also separated based on its involucrate inflorescence.

The third recent classification of Lauraceae (Richter, 1981) is not based on floral or fruit characters, but on wood and bark. It should therefore not be surprising that it differs in several features from Kostermans's and Hutchinson's classifications. Richter recognized three main groupings of genera without giving them taxonomic status. Each group includes primitive and more advanced genera (as defined by wood and bark characters). Ancestral genera from which these groups were derived are not yet known. The first group includes mostly palaeotropical genera—from this group only *Beilschmiedia*,

TABLE 2. *Classification of Lauraceae—Hutchinson (1964), neotropical genera.*

Tribe 1. <b>Apollonieae.</b> Inflorescence exinvolucrate; anthers two-celled; fruit not or partly enclosed by cupule. Flower bisexual. Fertile stamens 9; calyx usually persistent. <i>Beilschmiedia, Kubitzkia, Aniba, Nobeli dendron, Urbanodendron</i> Fertile stamens 6–3. <i>Aiouea, Licaria, Phyllostemonodaphne, Misanteca, Mezilaurus</i> Flowers dioecious or polygamo-dioecious. <i>Aniba, Endlicheria</i>
Tribe 2. <b>Cryptocaryeae.</b> Inflorescence exinvolucrate; anthers two-celled; fruit enclosed in floral tube. <i>Cryptocarya</i>
Tribe 3. <b>Sassafrideae.</b> Inflorescence exinvolucrate; anthers four-celled; all anther cells introrse. <i>Sassafridium</i> (now included in <i>Ocotea</i> )
Tribe 4. <b>Cinnamomeae.</b> As tribe 3, but at least one row of anthers with extrorse cells. Flowers bisexual. <i>Nectandra, Persea, Phoebe, Pleurothyrium, Caryodaphnopsis, Synandrodaphne (= Rhodostemonodaphne)</i> Flowers bisexual or polygamous <i>Ocotea, Dicypellium</i>
Tribe 5. <b>Litseaee.</b> Inflorescence involucrate; flowers umbellate or solitary within the involucre. Anthers four-celled. <i>Litsea, Umbellularia</i> Anthers two-celled. <i>Lindera, Laurus</i>
Tribe 6. <b>Cassytheae.</b> Parasitic, leafless herbs. <i>Cassytha</i>

*Caryodaphnopsis*, and *Cryptocarya* are represented in the New World, albeit with few species. The second group includes most of the genera occurring in the subtropics of the Northern Hemisphere (*Persea* is the exception), but several of the genera are best represented in tropical areas. This group is represented in the New World by *Litsea*, *Lindera*, *Sassafras*, and *Umbellularia*. The third group includes all other (15 or 16) neotropical genera plus a few paleotropical segregates of *Persea* and *Phoebe/Cinnamomum* (*Alseodaphne, Dehaasia, Neocinnamomum*, and *Nothaphoebe*). Within this group, *Persea*, *Cinnamomum*, *Phoebe*, and allies can be separated from the remaining endemic neotropical genera (*Ocotea* is also present in Africa and Madagascar), but the remaining genera do not fall in distinct groupings based on wood or bark characters.

The classifications by Kostermans and Hutchinson show that our knowledge of the relationships among the genera of Lauraceae is still limited. Essentially, these classifications are only keys to genera, often based on readily

observable but artificial characters such as the number of fertile stamens and number of anther cells on the stamens. The genera, defined with the help of these characters, often include species that do not possess the required characters but are placed in a certain genus due to general resemblance to other

TABLE 3. *Genera groups according to Richter (1981), neotropical genera.*

Group I	Group III
<i>Beilschmiedia</i>	<i>Persea</i>
<i>Cryptocarya</i>	<i>Phoebe</i>
<i>Caryodaphnopsis</i>	<i>Pleurothyrium</i>
	<i>Endlicheria</i>
Group II	<i>Aiouea</i>
<i>Lindera</i>	<i>Nectandra</i>
<i>Litsea</i>	<i>Ocotea</i>
<i>Umbellularia</i>	<i>Urbanodendron</i>
<i>Sassafras</i>	<i>Kubitzkia</i>
	<i>Dicypellium</i>
	<i>Licaria</i>
	<i>Aniba</i>
	<i>Anaueria</i>
	<i>Mezilaurus</i>
	[ <i>Rhodostemonodaphne</i> ]

species in that genus. Needless to say, this frustrates the efforts of the botanists who are not familiar with the group but try to key specimens to genus. A good example of these problems is found in the genus *Persea*. One of its characters is the presence of nine four-celled anthers and three staminodes. However, Kopp (1966), who monographed the genus, included in *Persea* also species with six four-celled anthers and six staminodes, and Kopp included species with some or all anthers two-celled, largely because of similarities in fruit and vegetative characters. In *Persea* the staminal configurations seem to be constant for a given species, but there are a few cases where the number of anther cells varies between flowers of the same inflorescence (*Aiouea lundelliana*, *Kubitzkia macrantha*). Normally, when flowers have both two- and four-celled anthers, the outer six anthers are always of one type and the inner three anthers the other; for instance, in *Endlicheria anomala* the outer six anthers are two-celled, the inner four-celled, while in *Phoebe* subg. *Heteranthera* the outer six are four-celled and the inner three are two-celled. Mez (1889) realized this and restricted the couplet in his generic key "anthers 4-celled or anthers 2-celled" to the outer six anthers. This greatly reduced the number of species that did not fit in any of the genera and made identifications easier. It is regrettable that this has been overlooked by later workers.

The differences in treatment of the genera with two-celled anthers show the lack of understanding of the generic relationships. In Hutchinson's classification, two-celled anthers characterize two tribes, the Apollonieae and Cryptocaryeae; the Cinnamomeae consist of four-celled genera, and the Litseae include both two- and four-celled genera. Thus, Hutchinson regarded the difference in number of anther cells as very important. Kostermans considered this difference as secondary, as all of his tribes include both two- and four-celled genera (except the monotypic Hypodaphneae), and accepted that the transition from four-celled to two-celled genera occurred several times. Richter found that wood and bark characters do not support the idea

that genera with two- and four-celled anthers form distinct groups, and it seems likely that the two-celled genera have been independently derived from four-celled genera. This theory is strengthened by the observation that in some two-celled neotropical genera the upper two cells have been lost, while in other genera the lower pair has disappeared. There are also indications that some two-celled genera (*Aiouea*, *Endlicheria*) are not monophyletic, but contain groups of species that were independently derived from four-celled ancestors; on the other hand, other two-celled genera of comparable size (*Aniba*, *Licaria*) seem to be monophyletic.

In addition to the differences in treatment of the two-celled genera, the three classification systems differ in many other details. Hutchinson and Richter recognized some neotropical genera that Kostermans did not accept. Examples are (from Hutchinson): *Sassafridium*, now accepted as belonging in *Ocotea*; *Nobeliodendron* and *Misanteca*, both now included in *Licaria* (Kurz, 1983); and *Synandrodaphne*, included in *Ocotea* by Kostermans (1957), also frequently included in *Nectandra* but recently recognized as *Rhodostemonodaphne* by Rohwer & Kubitzki (1985). Richter also recognized several genera that Kostermans had treated as synonyms: *Caryodaphnopsis*, *Nectandra*, *Pleurothyrium*, and *Anaueria*. More differences exist in the placement of the genera, largely because Kostermans and Hutchinson used different characters to define their tribes. For instance, Hutchinson placed most two-celled, exinvolucrate genera in the tribe Apollonieae, whereas in Kostermans's system these genera are divided between the Perseae and Cinnamomeae. Kostermans's Perseae are divided between Hutchinson's Apollonieae and Cinnamomeae. Although both classifications need to be modified, incorporating results from Richter's work, it seems that Kostermans's system needs fewer changes and has the major groups better defined than Hutchinson's system.

Both Kostermans's and Hutchinson's classifications are essentially keys and aimed at easing the identification of specimens to ge-

neric level. Information needed for an understanding of the phylogeny was (and is) not available. As has been mentioned earlier, workable keys to the genera are still not available and a large obstacle is that both floral and fruit characters are important for the definition of the genera although rarely specimens include flowers and fruits. This difficulty is not likely to be solved in the near future. It is possible to write a generic key based on floral characters with which most specimens can be identified. Fruiting material can be recognized either by cupule shape or leaf venation; cupules are likely to offer important characters for defining phylogenetically sound genera.

Difficulties in resolving the phylogenetic relationships should be viewed as distinct from difficulties involving identifications. Analyses of flower and fruit types have shown an extensive reticulate pattern of variation within the Lauraceae, and it is not known which taxa are primitive and which are derived, nor where the family originated. Raven & Axelrod (1974) postulated that, based on present patterns of distribution and endemism and on the fossil record, in the New World some taxa migrated from South America northward, while others, of Laurasian origin, were present in North America and moved southward. Gentry (1982) supported the hypothesis that the Lauraceae are a tropical Gondwanaland family. Richter's (1981) work on wood and bark anatomy has shown that the mostly small genera found in temperate and subtropical parts of the Northern Hemisphere (*Apollo-nias*, *Laurus*, *Lindera*, *Litsea*, *Sassafras*, and *Umbellularia*) have a similar wood structure. Because these genera occur in different continents, and because two other genera, now largely represented in the tropics, also occur in northern subtropical/temperate areas (*Ocotea* in the Canary Islands; *Persea* in North America and the Canary Islands), it is tempting to regard the Lauraceae as a Laurasian family that has very successfully spread into the tropics. The fact that *Ocotea* is much better represented in the tropics than in the temperate zones does not imply a tropical origin. Accepting the dioecious species as de-

rived from species with hermaphrodite flowers, one should note that most *Ocotea* species in the South American lowlands are dioecious, whereas nearly all Central American *Ocotea* species and most Andean species have perfect flowers. Further, in Central America *Ocotea* is much more weakly separated from its closest allies (*Nectandra*, *Phoebe*). These observations do not support the view that in the New World *Ocotea* and its allies originated in South America and moved north, but rather the reverse (Rohwer, 1986).

Much more information is needed for making secure claims about the phylogeny of the Lauraceae. First of all, our knowledge about the distribution of the genera is incomplete. Recently *Caryodaphnopsis*, previously known as an Asian genus of seven species, was found in South America (van der Werff & Richter, 1985); recent collections show that this genus includes six to eight neotropical species and occurs in Costa Rica, Panama, Colombia, Ecuador, Peru, and Brazil. Also during the last few years, four genera previously not known from Central America have been discovered there (*Aniba*, *Caryodaphnopsis*, *Mezilaurus*, and *Pleurothyrum*; pers. obs.).

Characters beyond flowers and fruits should be investigated. An excellent example is the work by Richter (1981) on wood and bark anatomy; studies of pollen, such as here reported, are very promising, and a study of leaf venation (Klucking, 1987) will appear soon. Other areas worthy of investigation are the chemical constituents and the structure of the cuticles. Results of such studies will be of much help in assessing the importance of the various morphological characters and in determining which characters should be used to define monophyletic genera and which are important on the species level.

#### PALYNOLOGICAL REVIEW

Extensive palynological investigations have been few. These were based mostly on observations with light microscopes. Pollen-morphological studies have been made by classical and by recent workers. The former generally

included information on pollen as a matter of secondary importance.

The history of pollen descriptions probably began with Kölreuter (1811), followed by Purkinje (1830), Fritzsche (1832), Mohl (1834), Schnizlein (1843–1870), Berg & Schmidt (1858), Griffith & Henfrey (1875), Edgeworth (1877), Mez (1888), Knell (1914), Armbruster & Oenike (1929), Wodehouse (1932, 1965), Zander (1935, 1937, 1941), Cranwell (1942, 1953), Selling (1947), Kasapliligil (1951), Erdtman (1952), Veloso & Barth (1962), and Pal (1976). The general descriptions given by the said authors is that the pollen grains are devoid of furrows and pores. Likewise, the sculpture spoken of by Wodehouse, as well as Mez, Knell, Zander, and Selling, to mention a few, are matters of controversy.

Short pollen descriptions and illustrations have also found a place in many regional floras: see Cranwell (1942, 1953), Ikuse (1956), Zinderen Bakker (1956), F. H. Wang (1960), J. L. Wang (1962, 1969), Rao & Lee (1970), Heusser (1971), Huang (1970, 1972), Markgraf & D'Antoni (1978), Lieux (1980), and Lewis et al. (1983).

Casual reference to pollen morphology mainly from an embryological standpoint has also been made by Schroeder (1952), Sastri (1958, 1962), Mitroiu (1970), and Pal (1975).

Recent noteworthy palynotaxonomic and phylogenetic studies are those of Agababian (1969, 1973), Ghosh (1977), Suryanarayana & Deodikar (1978), and Datta & Chanda (1980).

Of late the specialized wall structure of pollen grains has attracted the attention of many workers such as Takeoka (1965), Walker (1976), Rowley & Vasanthi (1980), Kubitzki (1981), Hesse & Kubitzki (1983), Hesse & Waha (1983), and Sohma (1985). The pollen wall is characteristic because of the extreme thinness of exine and the massive nature of the intine. A similar type of sporoderm stratification has been encountered in Cannaceae, Heliconiaceae, Hernandiaceae, Strelitziaceae, and Monimiaceae (Erdtman,

1952; Kress et al., 1978; Kress & Stone, 1982, 1983a, b; Stone et al., 1979, 1981; Stone, 1987; Rowley & Skvarla, 1974, 1975, 1986; Foreman & Sampson, 1987).

There is a scanty pollen record of fossil lauraceous genera. The few recorded are those of Macko (1959) and Macphail (1980). It is interesting that Selling (1947) stated that it is not "as if it [lauraceous pollen] had been overlooked, nor do I think that the possibility of the pollens being easily destroyed and therefore rarely preserved in peat (as was suggested by Rudolph 1936, p. 297, with regard to the pollens of this family) is of importance for the interpretation of their absence."

The present study is a broadly based pollen-morphological investigation of the apparently eurypalynous family. The aim is to present detailed morphological descriptions based on light microscopy (LM) and scanning electron microscopy (SEM), as the previous works are limited to very brief, sometimes incorrect accounts, depending mostly on light microscope observations. The complicated exine structure, sculpture, and ultrastructural details can be adequately studied with scanning electron microscopy and transmission electron microscopy (TEM) only.

The present investigation is aimed not only at giving a better understanding of pollen morphology but also at determining the correctness of the grouping of different genera under different tribes, subtribes, and their subfamilies respectively. The deflections of the palynological compass needle, at times oversimplified, have been taken into account to see whether it points towards better grouping, rearrangement, affinities, or evolutionary tendencies among the genera investigated.

#### MATERIALS AND METHODS

Polliniferous material of all the species investigated (except one sample each of *Kubitzkia mezii* and *Mezilaurus navalium*, obtained from Kew) was collected from the herbarium of the Missouri Botanical Garden

(MO), St. Louis, Missouri, U.S.A. Permanent slides were made from unacetolyzed, fuchsin-stained pollen grains. Acetolysis easily disintegrates the pollen grains because of the extreme thinness of exine (Erdtman, 1943).

A total of 80 species belonging to 17 out of the known 22 neotropical genera have been investigated. The LM studies were made using a Leitz Wetzlar Dialux microscope with apochromatic oil immersion objective ( $\times 100$ , N.A. 1.32) and periplan eye pieces (GF  $\times 10$ ). Measurements were made under oil immersion and are based on 30 or more pollen grains per species. Exine thickness was measured in the center of mesocolpia of pollen grains lying in equatorial view and includes spinules and other exinous excrescences. The maximum and minimum numbers of spinules per species were calculated using a programmable computer (Texas Instruments II Programmable 59; for details see Christensen, 1986) and are presented in Table 1.

Pollen descriptions are based on LM and SEM observations. A general description is given for each genus, followed by a TEM description of the taxa sectioned. Pollen morphological data of the species are compiled in Table 1. The classification and order of genera follows that of Kostermans (1957), and the species are arranged in alphabetical order. The arrangement of photographs is according to the classification.

For scanning electron microscopy, unacetolyzed pollen grains were suspended in a drop of absolute alcohol and transferred to brass stubs. The pollen grains were coated with gold palladium for seven minutes using a Fine Coat ION Sputter JFC-II00. Scanning micrographs were taken with a Jeol JSM 25S-II microscope using Ilford FP4 film.

For transmission electron microscopy, unacetolyzed anthers were fixed in TAG solution (Rodewald & Karnovsky, 1974), buffered in sodium cacodylate buffer, postfixed in osmium tetroxide, and embedded in Spurr. Ultrathin sections were cut with a diamond knife using an LKB ultratome and poststained with uranyl acetate and lead citrate. The terminology follows that of Erdtman (1969).

## GENERIC DESCRIPTIONS

The pollen grains of all the species investigated are inaperturate and spheroidal. The exine consists of an extremely thin, continuous or interrupted layer with an ornamentation consisting of pointed or blunt spinules made up of numerous twisted strands or of minute processes of varying shape (except *Cryptocarya*, where the exine is thin and smooth). The thinness of the exine makes it exceedingly difficult to distinguish the sexinous layer from the nexinous layer. Ultrastructural study of the pollen wall leads to the conclusion that the exine is totally ectexinous. The dominant massive layer is the intine. It is stratified, and its composition can be fibrillar, lacunar, lamellated, or granular. The intinous nature of this layer has been verified by acetolysis. It is uniformly thick throughout and does not show special thickenings that indicate possible germinal exits or germinative zones at any place. Instead, the entire wall may be equally suited for pollen tube egress.

*Persea*. Figure 1.

Diameter of pollen grains 29–44  $\mu\text{m}$ . Exine 0.5–1.5  $\mu\text{m}$  thick, scattered with spinules 1–3  $\mu\text{m}$  apart of faintly discernible twisted strands. Spinules < 0.5–ca. 1  $\mu\text{m}$  long, pointed or blunt, monomorphic or dimorphic with a basal cushionlike form of irregular shape; spinule surface devoid of processes but surrounded by a ring of densely spaced processes of varying shape and size. Intine 3–4  $\mu\text{m}$  thick, appearing homogeneous.

In *P. americana* and *P. mutisii* the spinules are dimorphic; blunt and pointed spinules are intermingled. In *P. caerulea* and *P. schiedeana* the pollen grains are dimorphic; one type of pollen grains has monomorphic spinules and the other dimorphic. In *P. veraguasensis* neither the pollen grains nor the spinules are dimorphic.

*Persea fulva*. Figure 1C. TEM observation: pollen wall 4  $\mu\text{m}$  thick, its outer, very thin electron-dense layer consisting of globular elements or in places baculalike elements



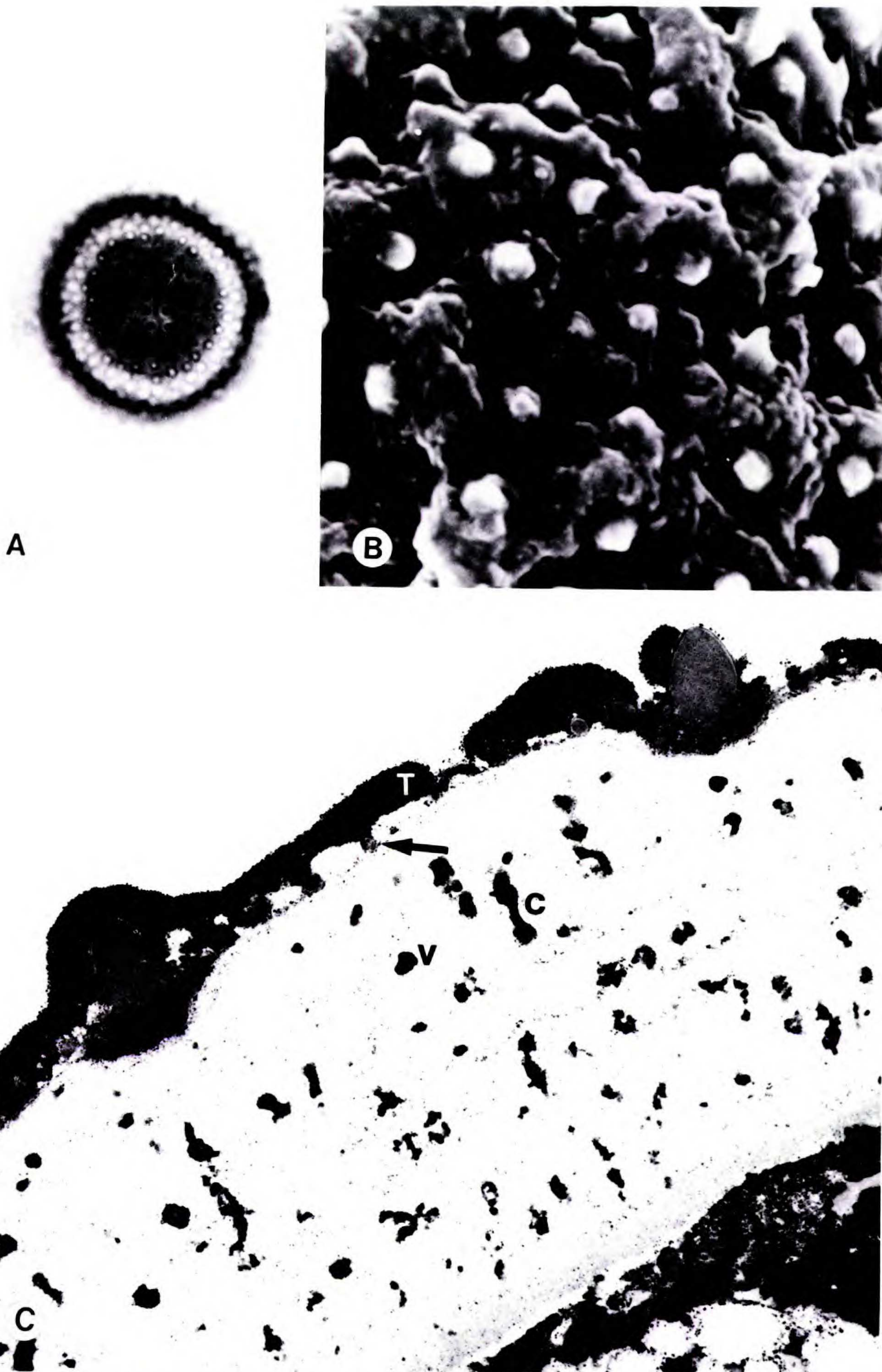


FIGURE 1. *A, B. Persea americana.*—*A.* Entire pollen grain; spinules appear as white dots in the peripheral region; at a lower focus in the middle they appear as dark dots. LM  $\times 1,000$ .—*B.* Part of exine showing spinules and the cushionlike bases studded with minute processes. SEM  $\times 11,000$ .—*C.* *P. fulva.* Part of pollen wall showing the outer thin, electron-dense layer made up of globular or in places baculalike elements (arrow) supporting a discontinuous tectum (*T*). The underlying intinous layer shows channels (*c*) and vacuoles (*v*). TEM  $\times 20,000$ .

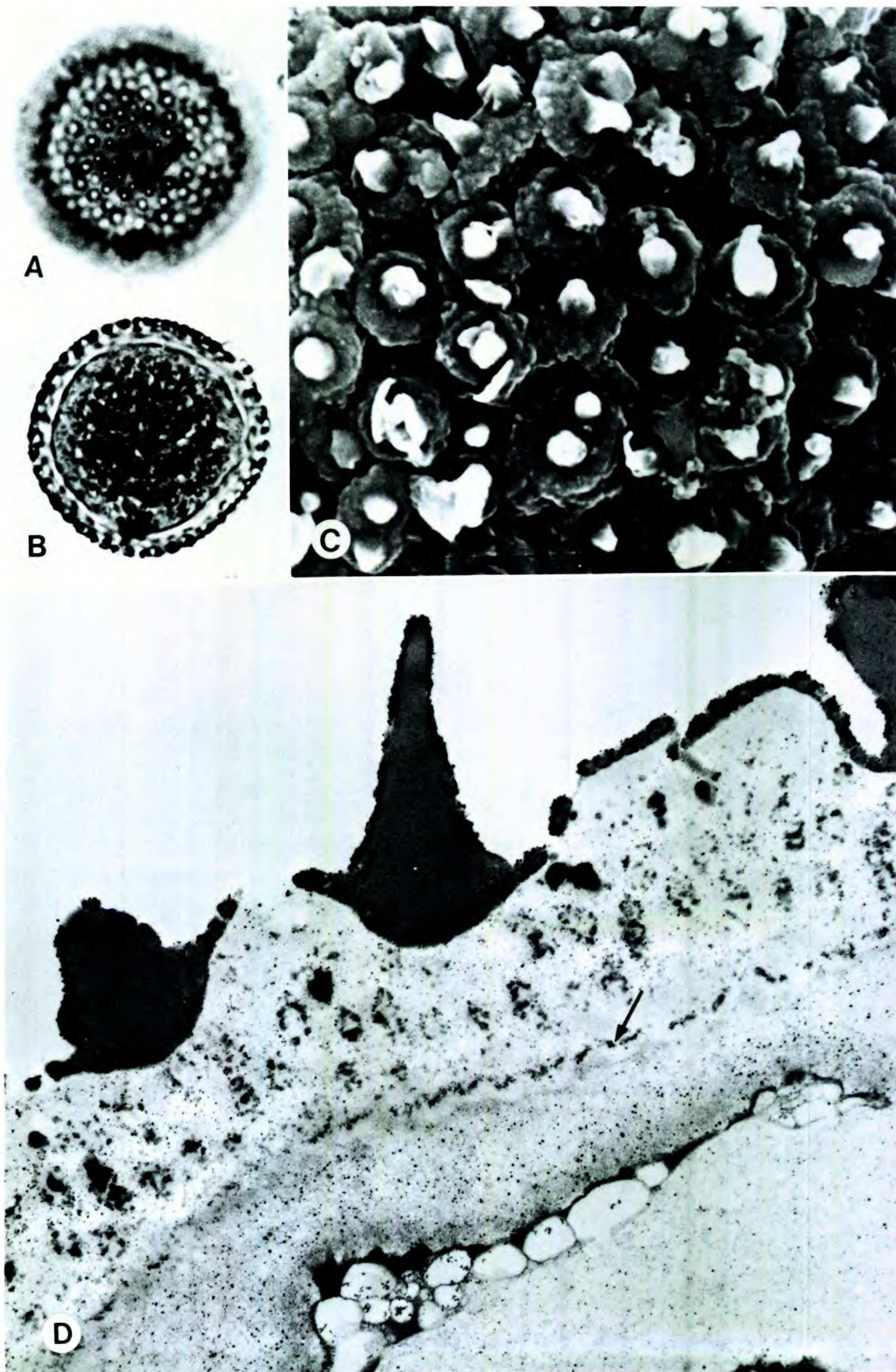


FIGURE 2. A-C. *Phoebe porphyria*.—A. Entire pollen grain, surface view showing densely spaced spinules as white dots.—B. The same in optical cross section. LM  $\times 1,000$ .—C. Part of exine showing spinules and their basal, circular cushion, its surface scattered with a few minute granular processes. SEM  $\times 11,000$ .—D. *P. helicterifolia*. Part of pollen wall showing details of stratification. TEM  $\times 20,000$ . Note the thin, interrupted commissural line (arrow) demarcating the outer and inner intine layers.

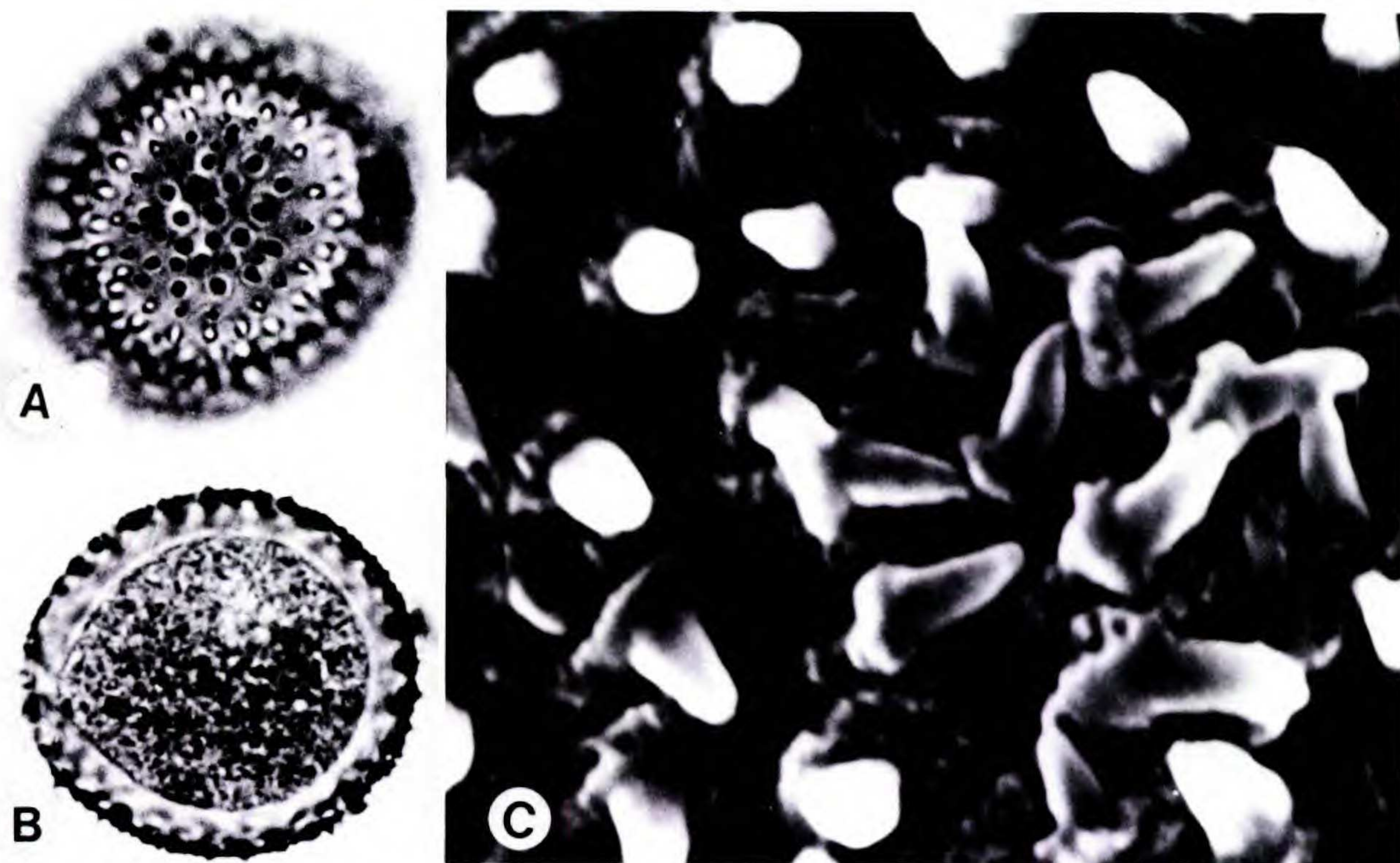


FIGURE 3. *Caryodaphnopsis fosteri*.—A. Entire pollen grain; spinules appear as white dots in the peripheral region; at a lower focus in the middle they appear as dark dots.—B. The same in optical cross section. LM  $\times 1,000$ .—C. Part of exine showing spinules and their basal cushion, the surface covered with granular processes. SEM  $\times 11,000$ .

supporting a discontinuous tectum and minute, pointed, solid spinules  $3\ \mu\text{m}$  apart, with a prominent, circular basal cushion intruding into the intinous layer, surrounded by densely spaced globular elements. The spinules and exinous surface covered with a “fuzzy coating” of granular composition. The underlying massive intinous layer distinguished into an outer, thick fibrillar layer with irregularly oriented narrow channels and vacuoles filled with osmiophilic material and into an inner, thin, electron-dense granular layer with a slightly undulating inner margin.

*Phoebe*. Figure 2.

Diameter of pollen grains  $21\text{--}33\ \mu\text{m}$ . Exine  $1\text{--}2\ \mu\text{m}$  thick, scattered with spinules  $1\text{--}2.5\ \mu\text{m}$  apart of easily discernible twisted strands. Spinules  $< 1\text{--}2\ \mu\text{m}$  long, pointed, with a prominent basal, circular, cushionlike form. These cushionlike forms densely spaced, their surface and the general surface of exine scattered with sparsely spaced, minute, granular processes.

*Phoebe helicterifolia*. Figure 2D. TEM observation: pollen wall  $5\ \mu\text{m}$  thick, differ-

entiated into an outer, thin, electron-dense ornamented exinous layer composed of closely packed granular elements and minute, pointed, spinules  $2\ \mu\text{m}$  apart, with a distinct, circular basal cushion intruding deeply into the intinous layer and making its distal surface distinctly undulating. Spinules and exinous surface covered with a “fuzzy coating.” The underlying massive intinous layer distinctly demarcated into an outer, relatively thick, distally undulating layer beset with usually radially oriented cavities, these partly filled with osmiophilic material, and into an inner, unevenly thickened, electron-dense fibrillar layer, its inner margin uneven. The outer and inner layers of intine clearly separated by a thin, discontinuous electron-dense commissural line.

*Caryodaphnopsis*. Figure 3.

Diameter of pollen grains  $27\text{--}33\ \mu\text{m}$ , rarely  $41\ \mu\text{m}$ . Exine  $2\ \mu\text{m}$  thick, scattered with simple spinules  $2\text{--}3\ \mu\text{m}$  apart (rarely the spinules show faintly discernible twisted strands). Spinules about  $1.5\ \mu\text{m}$  long, pointed, with a basal cushionlike form, this circular to irreg-

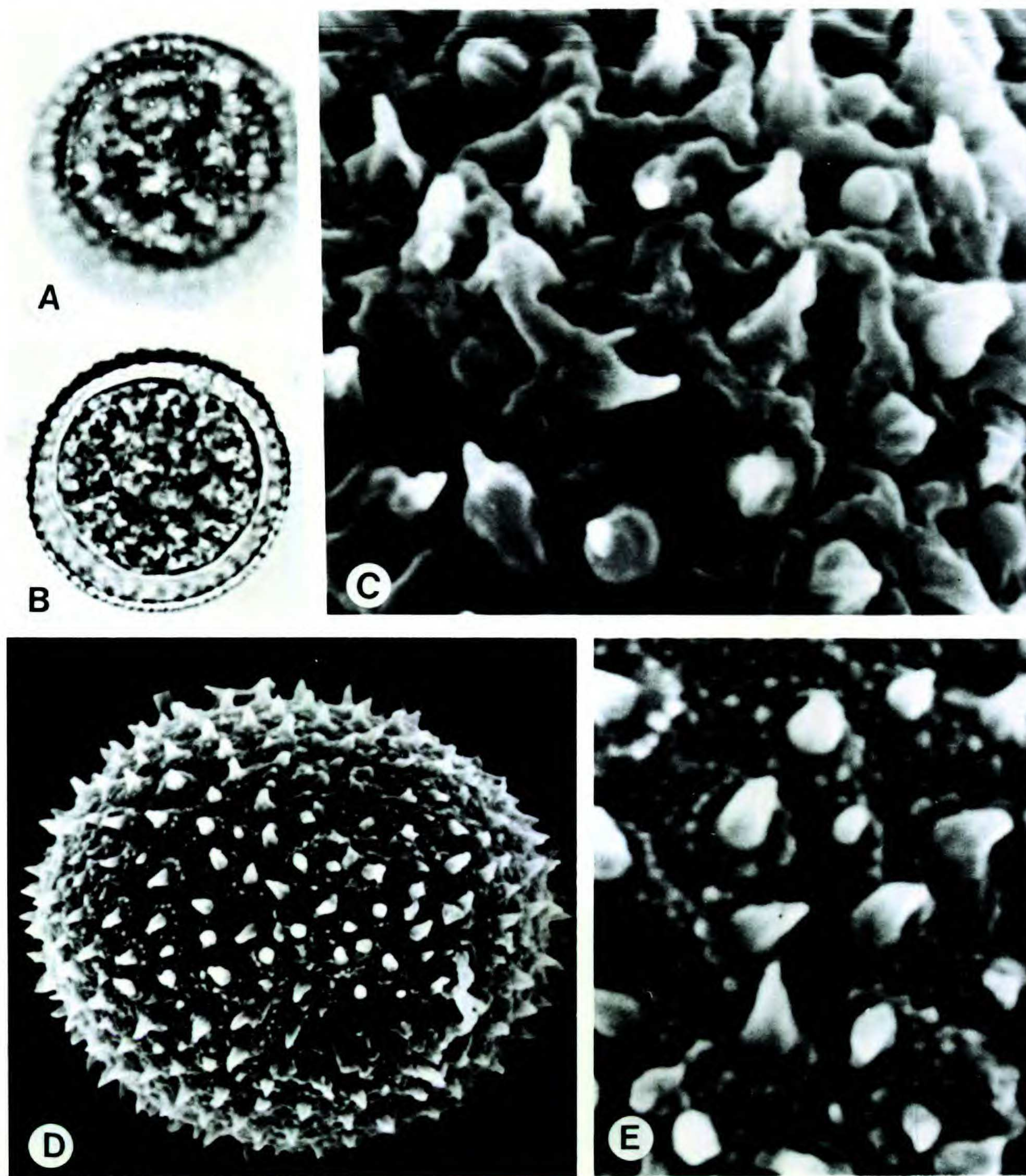


FIGURE 4. A–C. *Beilschmiedia pendula*.—A. Entire pollen grain showing spinules as white dots.—B. The same in optical cross section. LM  $\times 1,000$ .—C. Part of exine beset with spinules, their basal cushionlike form devoid of granular processes. SEM  $\times 11,000$ . D, E. *Mezilaurus navalium*.—D. Entire pollen grain showing spinules, their basal cushions beset with minute processes. SEM  $\times 3,300$ .—E. Part of the same at a higher magnification. SEM  $\times 11,000$ .

ular in shape, its surface devoid of processes. The general surface of exine sparsely covered with minute processes. Intine  $2\ \mu\text{m}$  thick, appearing homogeneous.

*Beilschmiedia*. Figure 4A–C.

Diameter of pollen grains  $23\text{--}38\ \mu\text{m}$ . Exine  $1\text{--}2\ \mu\text{m}$  thick, scattered with spinules  $2\text{--}3\ \mu\text{m}$  apart of easily discernible twisted strands.

Spinules  $1\text{--}1.5\ \mu\text{m}$  long, pointed, with a basal cushionlike form of irregular shape; its surface and the general surface of exine devoid of processes. Intine  $2.5\text{--}5\ \mu\text{m}$  thick, appearing homogeneous.

*Mezilaurus*. Figure 4D, E.

Diameter of pollen grains  $22\text{--}26\ \mu\text{m}$ . Exine  $> 1\ \mu\text{m}$  thick, scattered with spinules  $2$

$\mu\text{m}$  apart of easily discernible twisted strands. Spinules  $< 0.5 \mu\text{m}$  long, pointed, with an ill-defined basal cushionlike form; its surface and the general surface of exine beset with densely spaced processes. Intine  $2 \mu\text{m}$  thick, appearing homogeneous.

*Ocotea*. Figure 5.

Diameter of pollen grains  $17\text{--}39 \mu\text{m}$ . Exine  $1\text{--}2.5 \mu\text{m}$  thick, scattered with spinules  $1\text{--}4 \mu\text{m}$  apart of distinctly discernible twisted strands. Spinules  $< 0.5\text{--}2 \mu\text{m}$  long, pointed or blunt with well-defined, thick, basal, circular, cushionlike form, its surface uneven. The cushionlike forms densely spaced and each surrounded by a ring of partially fused elements of varying size and shape. The general surface of exine beset with small processes of varying size and shape.

In a few species, such as *O. cernua* and *O. ira*, transparent porelike or colpuslike areas devoid of spinules occur. In *O. cuprea* the pollen grains are dimorphic; one type of pollen grain has pointed spinules made up of twisted strands, with a prominent, circular, basal cushionlike form. These cushionlike forms are densely spaced and appear as small islands surrounded by partially fused, small, globular processes. In places five or six spinules are grouped on a single cushion. In the second type of pollen grain, the spinules are pointed and broad basally but without a basal cushionlike form. The intine is  $2\text{--}5 \mu\text{m}$  thick and homogeneous to many layered.

*Ocotea puberula*. Figure 5C. TEM observation: pollen wall  $4 \mu\text{m}$  thick, differentiated into an outer, very thin, electron-dense ornamented exinous layer composed of minute, closely packed globular elements and minute, pointed, solid spinules,  $3 \mu\text{m}$  apart with a distinct, circular basal cushion slightly intruding into the intinous layer and surrounded by densely spaced globular elements. The spinules and general exinous surface covered with a "fuzzy coating." The underlying massive intinous layer clearly distinguished into an outer, relatively thick layer beset with narrow, radially oriented channels in contact

with the surface, these partly filled with bead-shaped osmiophilic material, and into a relatively thin, electron-dense, rather homogeneous layer of varying electron density, its inner margin irregular.

*Nectandra*. Figure 6.

Diameter of pollen grains  $18\text{--}33 \mu\text{m}$ . Exine  $0.5\text{--}1.5 \mu\text{m}$  thick, scattered with spinules  $1\text{--}4 \mu\text{m}$  apart of faintly discernible twisted strands. Spinules  $0.5\text{--}1.5 \mu\text{m}$  long, pointed, with a distinct, basal, circular to irregular cushionlike form, its surface and the general surface of exine devoid of processes.

In *N. ambigens* the spinules are crowded in places to form a rosettelike pattern or are sometimes found in pairs on a common basal cushion. In *N. falcifolia* the spinules are frequently crowded in places or are dimorphic. In *N. grandis* they are blunt and vestigial. The intine  $1\text{--}4 \mu\text{m}$  thick and homogeneous or apparently bizonal or lamellated.

*Nectandra gentlei*. Figure 6E. TEM observation: pollen wall  $5 \mu\text{m}$  thick, its outer, very thin, electron-dense, ornamented exinous layer composed of closely packed granular to globular elements and minute, pointed, solid, spinules  $1 \mu\text{m}$  apart with a distinct, circular, basal cushion intruding into the underlying layer. The underlying massive intinous layer made up of an upper, relatively thick layer beset with ill-defined narrow channels partly filled with osmiophilic material and of an inner, relatively thin, many-layered granular stratum of varying electron density, its inner margin very irregular.

*Pleurothyrium*. Figure 7.

Diameter of pollen grains  $21\text{--}30 \mu\text{m}$ . Exine  $0.5 \mu\text{m}$  thick, scattered with spinules  $1\text{--}2 \mu\text{m}$  apart of easily discernible twisted strands. Spinules  $< 0.5 \mu\text{m}$  long, pointed, with a prominent, basal, circular cushionlike form, totally or partially surrounded by a ring of densely spaced, partially fused minute processes. The general surface of exine beset with sparsely

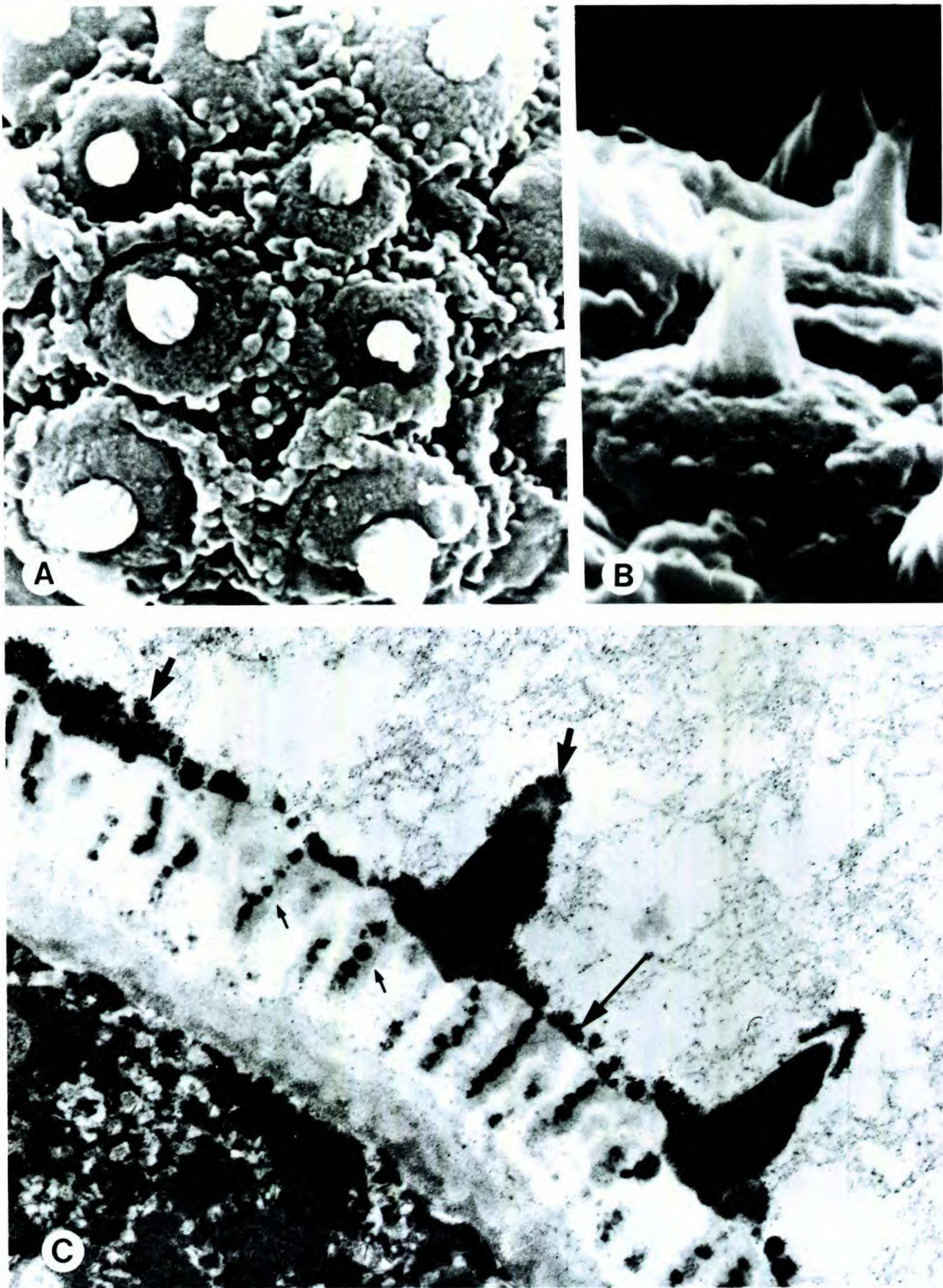


FIGURE 5. *A, B. Ocotea cuprea.*—*A.* Part of exine showing spinules, circular, cushionlike smooth form, surrounded by densely spaced minute processes. SEM  $\times 11,000$ .—*B.* Part of the same showing a few spinules and details of their basal part. Note the twisted strands of the spinules. SEM  $\times 22,000$ .—*C. O. puberula.* Part of pollen wall differentiated into an outer thin, electron-dense layer, composed of globular elements (long arrow). Note the spinules and exine covered with a "fuzzy coating" (thick, short arrows); radially oriented channels filled with bead-shaped osmiophilic material (small, thin arrows). TEM  $\times 20,000$ .

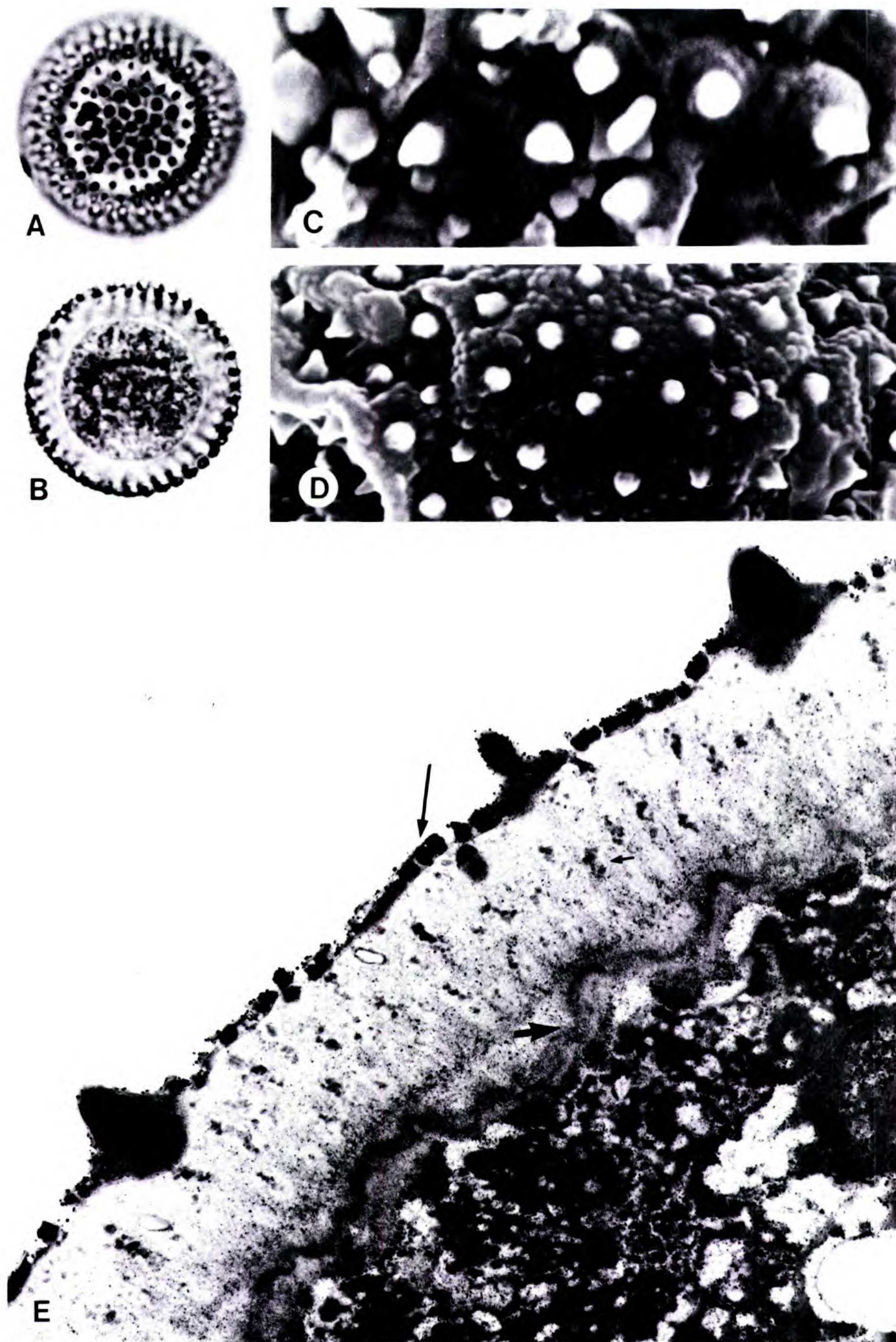


FIGURE 6. *A-C.* *Nectandra reticulata*.—*A.* Entire pollen grain showing spinules as white dots in the peripheral region and as dark dots in the middle.—*B.* The same in optical cross section. *LM*  $\times 1,000$ .—*C.* Part of exine showing spinules and their smooth, basal cushionlike form. *SEM*  $\times 11,000$ .—*D.* *Rhodostemonodaphne grandis*. Part of exine showing a surface pattern dissimilar to *N. reticulata*. *SEM*  $\times 11,000$ .—*E.* *Nectandra gentlei*. Part of pollen wall showing the outer thin, electron-dense layer made up of granular to globular elements (arrow).

spaced, minute processes. Intine 1.5  $\mu\text{m}$  thick, appearing homogeneous.

*Pleurothyrium zulianense*. Figure 7D. TEM observation: pollen wall 2  $\mu\text{m}$  thick, its outer thin, electron-dense ornamented exinous layer made up of granular to globular elements and minute, pointed, solid spinules 1  $\mu\text{m}$  apart with a distinct, circular, basal cushion intruding into the intinous layer. The underlying massive intinous layer distinguished into an outer thick, structurally loose, granular stratum bearing closely packed, narrow, radially oriented channels filled with osmiophilic material and into an inner, thin, granular layer, its margin irregular.

*Umbellularia*. Figure 8.

Diameter of pollen grains 31–36  $\mu\text{m}$ . Exine 1  $\mu\text{m}$  thick, scattered with spinules 3  $\mu\text{m}$  apart of faintly discernible twisted strands. Spinules < 1  $\mu\text{m}$  long, pointed, with a prominent, basal, circular cushionlike form, partially surrounded by a ring of densely spaced, partially fused minute processes. The general surface of exine studded with densely spaced, minute processes of varying size and shape. Intine 2.5  $\mu\text{m}$  thick, appearing homogeneous.

*Umbellularia californica*. Figure 8D. TEM observation: pollen wall 6  $\mu\text{m}$  thick and consisting of an outer, thin, electron-dense ornamented exinous layer composed of densely spaced clavate to globular elements of varying size and of minute, solid, spinules 3  $\mu\text{m}$  apart with a distinct, circular basal cushion intruding deeply into the intinous layer, and surrounded by densely spaced globular elements of varying size. The spinules and general exinous surface covered with loose “fuzzy coating.” The underlying massive intinous region clearly distinguished into an outer, relatively thick stratum with scattered, radially oriented, ill-defined channels partly filled with

osmiophilic material and into an inner, relatively thin, granular layer of varying electron density, its inner margin smooth.

*Aiouea*. Figure 9.

Diameter of pollen grains 19–29  $\mu\text{m}$ . Exine 0.5  $\mu\text{m}$  thick, scattered with spinules 1–3  $\mu\text{m}$  apart of very faintly discernible twisted strands. Spinules 0.5  $\mu\text{m}$  long, pointed, with a basal, thin, circular to irregularly shaped cushionlike form, frequently surrounded by a ring of densely spaced, partially fused, minute processes. Cushionlike forms usually fused, their surface uneven, devoid of processes. General surface of exine beset with sparsely spaced, minute processes. Intine 1.5–3  $\mu\text{m}$  thick and appearing homogeneous.

In *A. costaricensis* the pollen grains exhibit in places porelike transparent areas devoid of spinules.

*Aiouea trinervis*. Figure 9D. TEM observation: pollen wall about 4  $\mu\text{m}$  thick, differentiated into an outer, very thin, electron-dense ornamented exinous layer made up of compact granular elements and spinules. The spinules minute, pointed, solid, 1–3  $\mu\text{m}$  apart with a distinct, circular basal cushion intruding into the subtending layer, and surrounded by densely spaced globular elements of varying size. The underlying massive intinous stratum consisting of an outer, relatively thick, structurally loose fibrillar layer made up of vacuoles and channels filled with osmiophilic material and of a denser inner, 2–3-layered granular zone of varying electron density, its inner margin slightly irregular.

*Aniba*. Figure 10A–C.

Diameter of pollen grains 16–27  $\mu\text{m}$ . Exine 0.5  $\mu\text{m}$  thick, scattered with spinules 1  $\mu\text{m}$  apart of faintly discernible strands. Spinules < 0.5  $\mu\text{m}$  long, pointed, without dis-

←

The upper part of the intinous layer is beset with ill-defined channels partly filled with osmiophilic material (thin arrow); in the lower part undulating layers of varying electron density are seen (thick arrow). TEM  $\times 22,000$



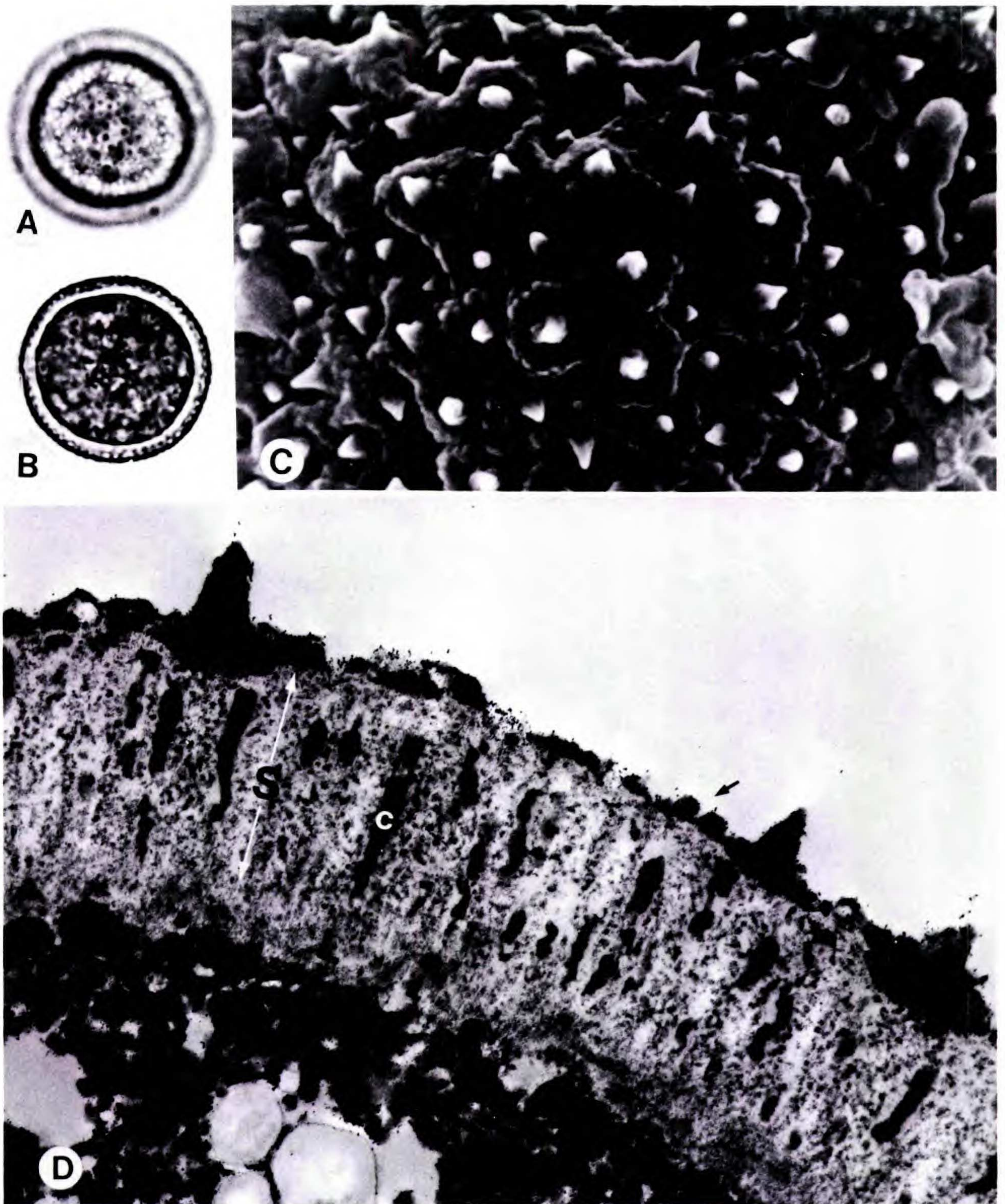


FIGURE 7. *A-C*. *Pleurothyrium densiflorum*.—*A*. Entire pollen grain showing spinules, white and dark dots.—*B*. The same in optical cross section. LM  $\times 1,000$ .—*C*. Part of exine showing surface details. SEM  $\times 11,000$ .—*D*. *P. zulianense*. Part of pollen wall showing the outer thin, electron-dense exinous layer made up of granular to globular elements (arrow) and showing the outer thick, structurally loose, granular stratum of intine (S) and an inner thin, granular layer (L). Note the radially oriented channels in the outer intine filled with osmiophilic material (c). TEM  $\times 20,000$ .

tinct, basal cushionlike forms. The general surface of exine densely spaced with granular processes. Intine 1.5–2  $\mu\text{m}$  thick and appearing homogeneous. In pollen grains of *A. formula* 2–3 porelike or irregular openings encountered.

*Endlicheria*. Figure 10D–F.

Diameter of pollen grains 15–27  $\mu\text{m}$ . Exine 0.5–1  $\mu\text{m}$  thick, scattered with spinules 0.5–2  $\mu\text{m}$  apart of faintly discernible strands. Spinules < 0.5–1  $\mu\text{m}$  long, densely or sparse-

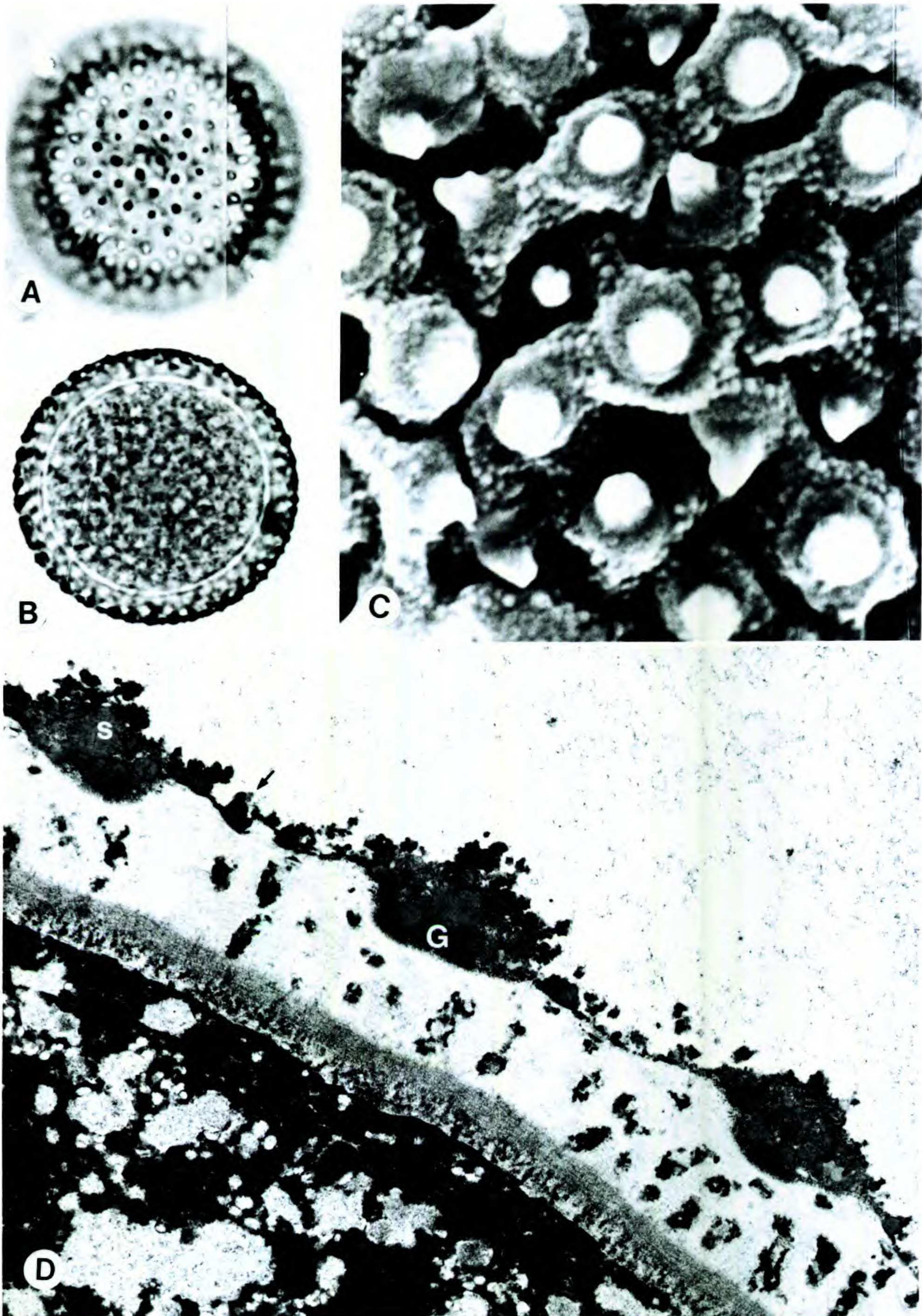


FIGURE 8. *Umbellularia californica*.—A. Entire pollen grain, showing spinules as white dots in the peripheral region and as dark dots in the middle.—B. The same in optical cross section. LM  $\times 1,000$ .—C. Part of exine showing spinules, their basal, circular, cushionlike form and the surrounding densely spaced, granular processes. SEM  $\times 11,000$ .—D. Part of pollen wall showing the outer, thin, electron-dense layer composed of clavate to globular elements (arrow) and spinules (s), their bases deeply intruding into the intine and surrounded by globular elements (G); spinules and exine surface covered with loose "fuzzy coating." The underlying thick, outer intine scattered with ill-defined channels partly filled with osmiophilic material; inner intine thin, granular, and of varying electron density. TEM  $\times 20,000$ .

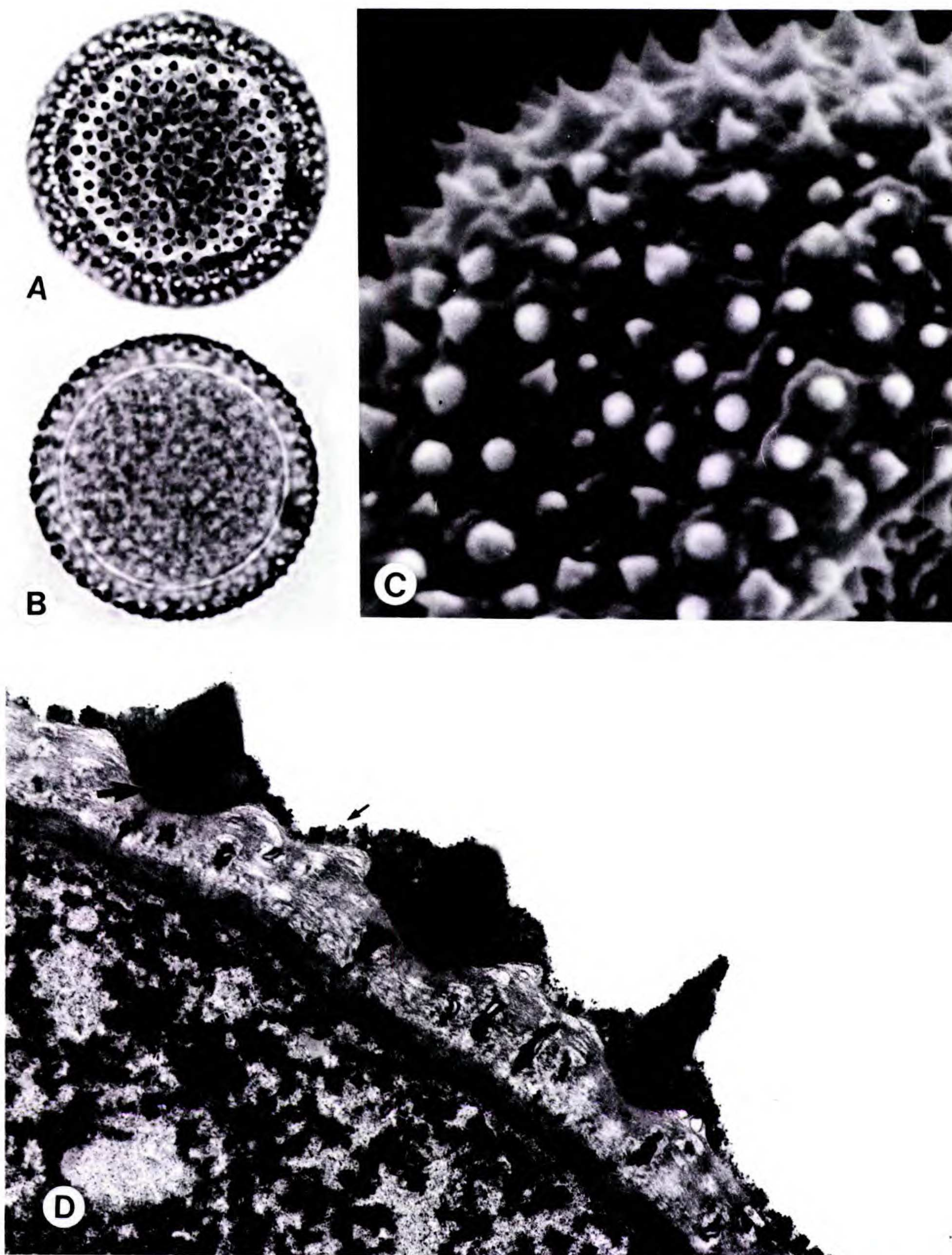


FIGURE 9. *A, B.* *Aiouea costaricensis*.—*A.* Entire pollen grain showing spinules as white dots in the peripheral region and as dark dots in the middle.—*B.* The same in optical cross section. LM  $\times 1,000$ . *C, D.* *A. trinervis*.—*C.* Part of exine showing surface details. SEM  $\times 11,000$ .—*D.* Part of pollen wall showing thin, electron-dense exinous layer made up of granular elements (thin arrow) and spinules, their bases intruding into the intine and surrounded by globular elements (thick arrow). Outer layer of intine fibrillar in composition and beset with radially oriented channels filled with osmiophilic material; inner layers denser, of varying electron density. TEM  $\times 20,000$ .

ly spaced, usually pointed, frequently vestigial. The basal cushionlike form of the spinules not easily discernible due to the surrounding densely spaced processes of

varying size and shape. General surface of exine beset with densely spaced, minute processes. Intine 1.5–2.5  $\mu\text{m}$  thick, appearing stratified.

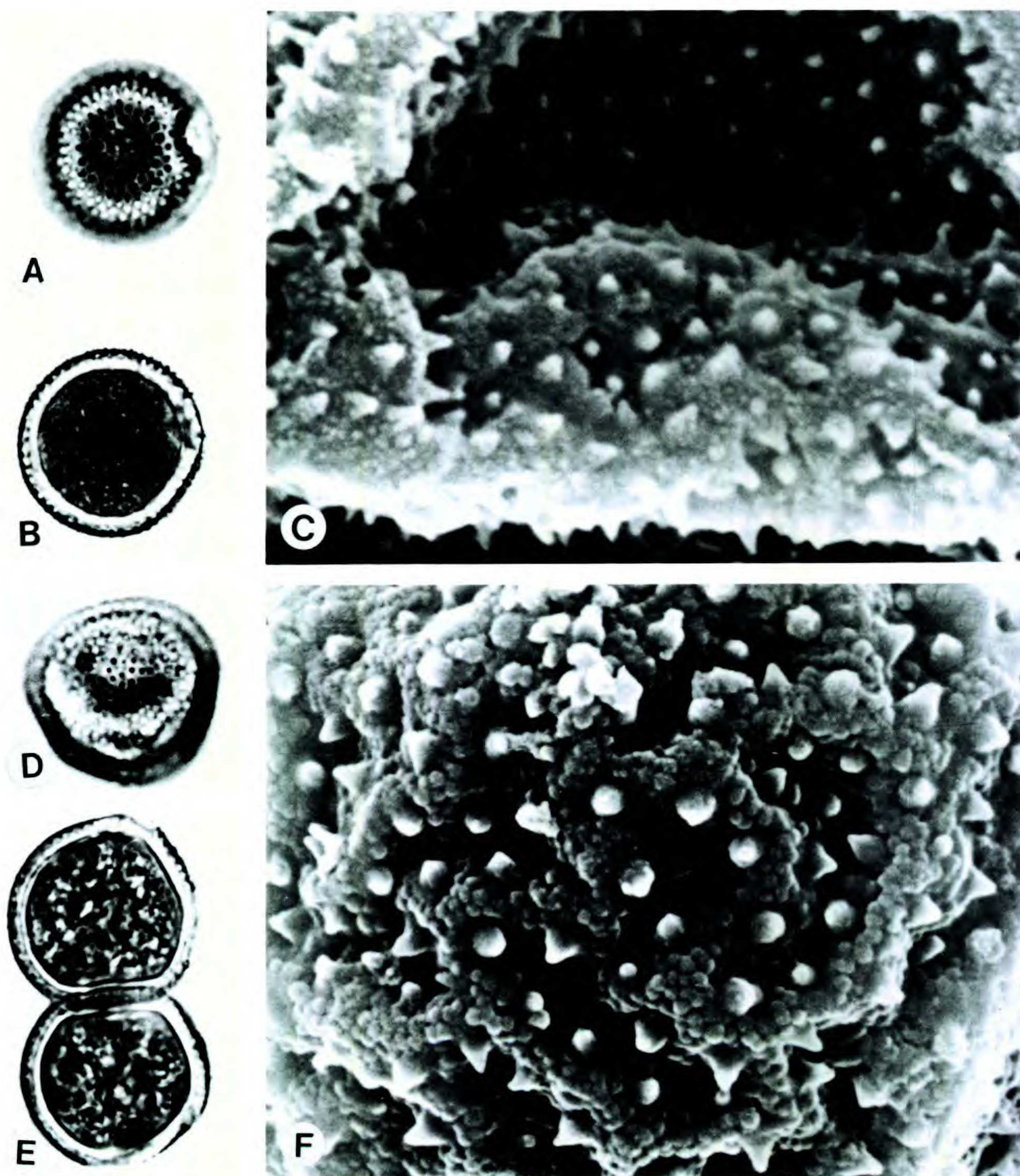


FIGURE 10. *A, B.* *Aniba burchellii*.—*A.* Entire pollen grain showing spinules as white dots in the peripheral region and as dark dots in the middle.—*B.* The same in optical cross section. LM  $\times 1,000$ .—*C.* *A. riparia*  $\times$  *A. kappleri*. Part of exine showing surface details. SEM  $\times 11,000$ . *D–F.* *Endlicheria endlicheriopsis*.—*D.* Entire pollen grain showing spinules as white dots in the peripheral region and as dark dots in the middle.—*E.* Two pollen grains in optical cross section. LM  $\times 1,000$ .—*F.* Part of exine showing spinules and the surrounding densely spaced processes. SEM  $\times 11,000$ .

*Endlicheria serica*. Figure 11A. TEM observation: pollen wall about 3  $\mu\text{m}$  thick, differentiated into an outer, very thin, electron-dense ornamented exinous layer composed of globular to granular elements, these appearing to fuse to form a thin tectum, and of minute, pointed, solid spinules 2  $\mu\text{m}$  apart with a distinct basal cushion intruding deeply into the underlying layer. The subtending

massive intinous layer loosely granular throughout, densely spaced with radially oriented channels partly filled with osmiophilic material, its inner margin more or less smooth.

*Licaria*. Figure 11B–D.

Diameter of pollen grains 17–33  $\mu\text{m}$ . Exine 0.5–1  $\mu\text{m}$  thick, scattered with spinules

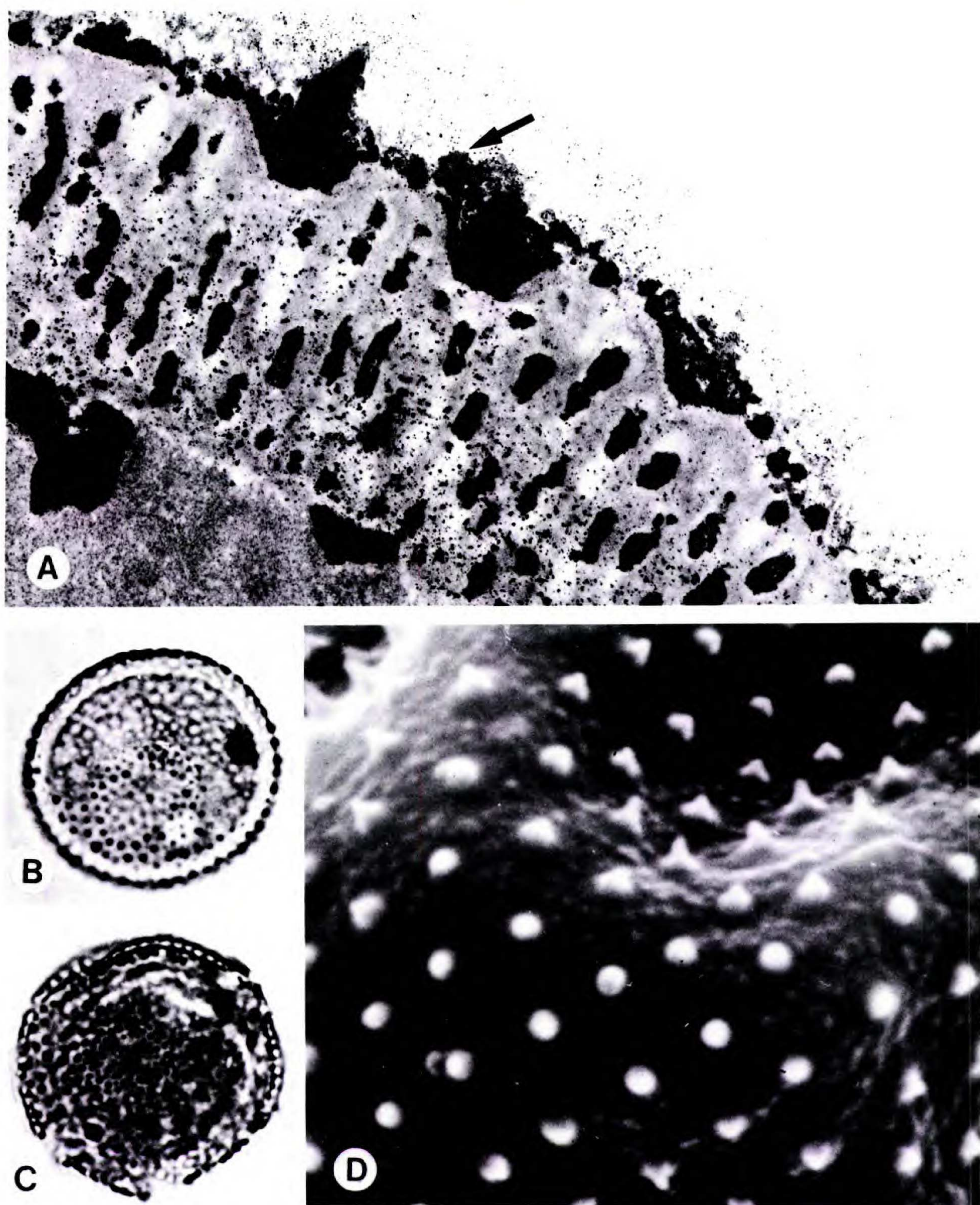


FIGURE 11.—A. *Endlicheria serica*. Part of pollen wall showing an outer thin, electron-dense exinous layer composed of granular to globular elements, which appear to form a thin tectum. Note traces of "fuzzy covering" on the surface of spinules and exine (arrow). Intine loosely granular throughout, beset with radially oriented channels, partly filled with osmiophilic material. TEM  $\times 20,000$ . B, C. *Licaria armeniaca*.—B. Entire pollen grain showing spinules as white and dark dots.—C. The same in optical cross section. LM  $\times 1,000$ .—D. *L. capitata*. Part of exine showing spinules and granular processes. SEM  $\times 11,000$ .

1–2  $\mu\text{m}$  apart of faintly discernible twisted strands. Spinules  $< 0.5 \mu\text{m}$  long, pointed, with a basal, circular, cushionlike form, surrounded by a ring of densely spaced, partially fused processes of varying size and shape. The general surface of exine beset with minute processes. Intine 1–3.5  $\mu\text{m}$  thick, appearing homogeneous.

*Licaria triandra*. Figure 12A. TEM observation: pollen wall 2  $\mu\text{m}$  thick, consisting of an outer, very thin, electron-dense, ornamented exinous layer composed of scattered or irregularly clustered granular elements and minute, pointed, solid spinules 1  $\mu\text{m}$  apart with a distinct basal cushion intruding into the underlying layer. The subtending massive

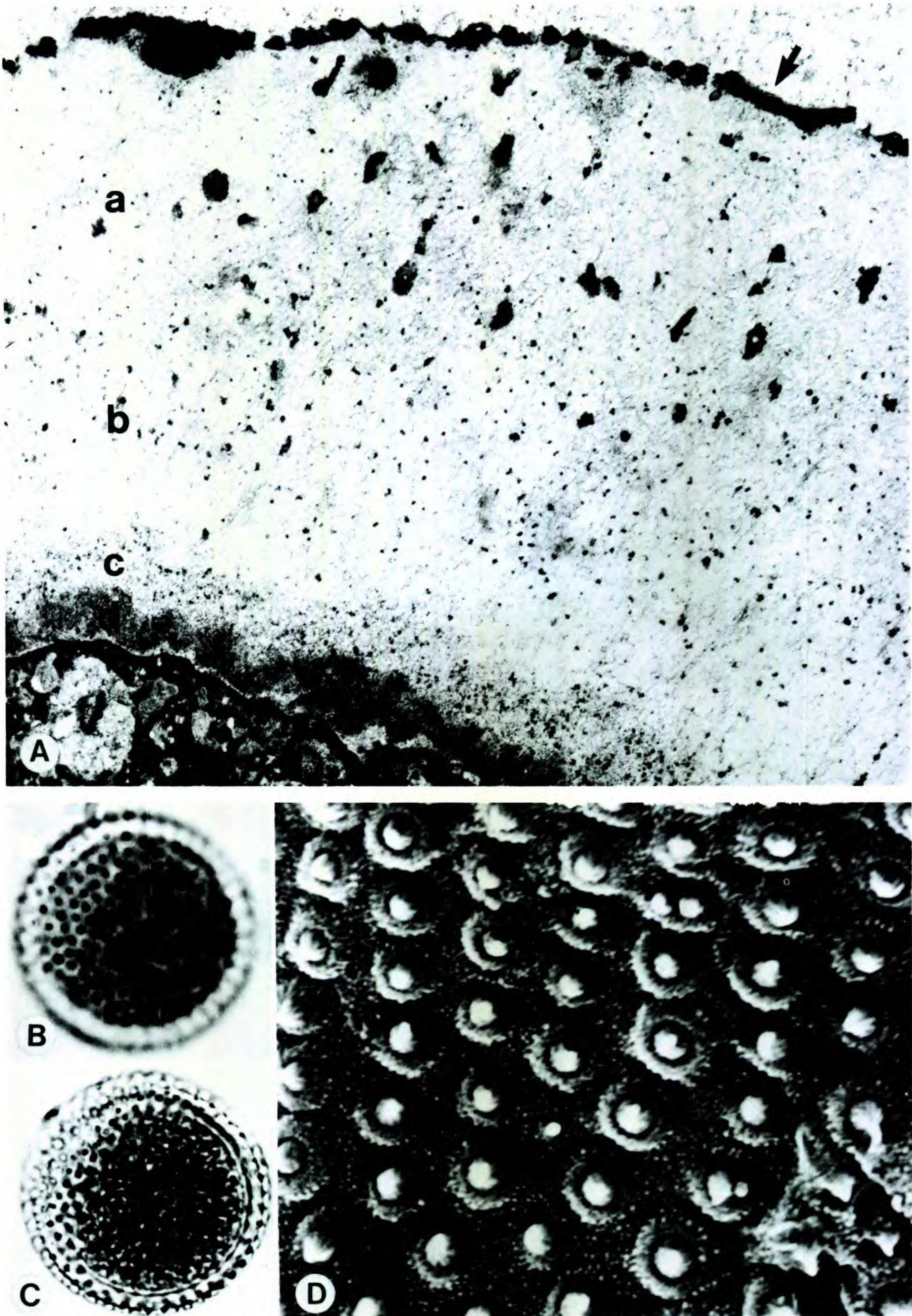


FIGURE 12.—A. *Licaria triandra*. Part of pollen wall showing an outer thin, electron-dense exinous layer (arrow). The underlying massive intinous layer differentiated into an outermost thick stratum, this fibrillar in composition with scattered narrow channels and with vacuoles filled with osmiophilic material (a); the second layer structurally loose and fibrillar, sprinkled with osmiophilic material (b); the third layer densely granular and sprinkled with osmiophilic material (c); the innermost layer denser than the other layers, extremely irregular in outline, structurally compact and granular (d). TEM  $\times 20,000$ . B–D. *Kubitzkia mezii*.—B. Entire pollen grain, spinules appear as dark dots (lower focus).—C. The same in optical cross section. LM  $\times 1,000$ .—D. Part of exine showing spinules and the surrounding granular processes. SEM  $\times 11,000$ .

intinous stratum made up of 4 distinct layers of varying composition. The outermost relatively thick, transversely organized, compact fibrillar layer with scattered, narrow channels and vacuoles partly filled with osmiophilic material. The second layer equally thick, less electron dense, structurally loose and fibrillar, sprinkled with osmiophilic material. The third layer is thinner, densely granular in composition, much more electron dense, and sprinkled in places with osmiophilic material. The layer next to the cytoplasmic boundary extremely irregular in outline, in places very thin or absent, and also much denser than the other layers, structurally compact and granular.

*Kubitzkia (Systemonodaphne)*.  
Figure 12B–D.

Diameter of pollen grains 24–27  $\mu\text{m}$ . Exine 1  $\mu\text{m}$  thick, scattered with spinules 2  $\mu\text{m}$  apart of easily discernible twisted strands. Spinules 0.5  $\mu\text{m}$  long, pointed, with a prominent basal, circular cushionlike form surrounded by a ring of densely spaced, partially fused processes of varying size and shape. The general surface of exine beset with densely spaced minute processes. Intine 3  $\mu\text{m}$  thick, appearing homogeneous.

*Litsea*. Figure 13.

Diameter of pollen grains 27–35  $\mu\text{m}$ . Exine 1  $\mu\text{m}$  thick, scattered with spinules 3  $\mu\text{m}$  apart of not easily discernible strands. Spinules < 1  $\mu\text{m}$  long, pointed with a basal cushionlike form, circular to irregular in shape and devoid of processes, partially surrounded by a ring of densely spaced, minute processes. Intine 4  $\mu\text{m}$  thick and appearing homogeneous.

*Litsea glaucescens*. Figure 13D. TEM observation: pollen wall 5  $\mu\text{m}$  thick, its outer, very thin, electron-dense, ornamented exinous layer composed of scattered or irregularly clustered granular to globular elements and of minute, pointed, solid spinules 3  $\mu\text{m}$  apart with a distinct basal cushion intruding into the intinous layer. The underlying massive

intinous layer distinctly distinguished into a thicker outer layer inlaid with channels and vacuoles filled with osmiophilic material and into a thinner, denser, homogeneous layer with a slightly uneven inner margin.

*Cryptocarya*. Figure 14.

Diameter of pollen grains 30–33  $\mu\text{m}$ . Exine 0.5–1  $\mu\text{m}$  thick, appears disrupted in optical cross section (in LM), its outer surface much wrinkled. Intine 2.5–4  $\mu\text{m}$  thick, appearing stratified.

*Cryptocarya aschersoniana*. Figure 14D. TEM observation: pollen wall about 4.5  $\mu\text{m}$  thick, its outer very thin, electron-dense stratum consisting of an uneven tectum supported by densely spaced clavatelike to globular elements and of a suprategal thin coating of compact material. The subtending massive intinous layer distinctly distinguished into an outer thick, less electron-dense, structurally loose, transversely organized fibrillar layer inlaid with scattered vacuoles, these partly filled with osmiophilic material, and into an inner electron-dense, structurally compact, transversely organized fibrillar layer interrupted by long, narrow channels filled with osmiophilic material. These channels traversing the entire thickness of the layer, conical in shape, and having an outlet into the layer above. The intinous layer next to the cytoplasmic boundary denser than the other layers and in places beset with narrow, short channels filled with osmiophilic material.

*Cassytha*. Figure 15.

Diameter of pollen grains 22–28  $\mu\text{m}$ . Exine 0.5  $\mu\text{m}$  thick, its surface scattered with minute, spinuloid excrescences. Intine 4  $\mu\text{m}$  thick, appears homogeneous.

## DISCUSSION

### GENERAL POLLEN-MORPHOLOGICAL FEATURES

The pollen grains of Lauraceae are inaperturate and more or less spheroidal. Kasaplilgil (1951), however, found monocolpate pollen

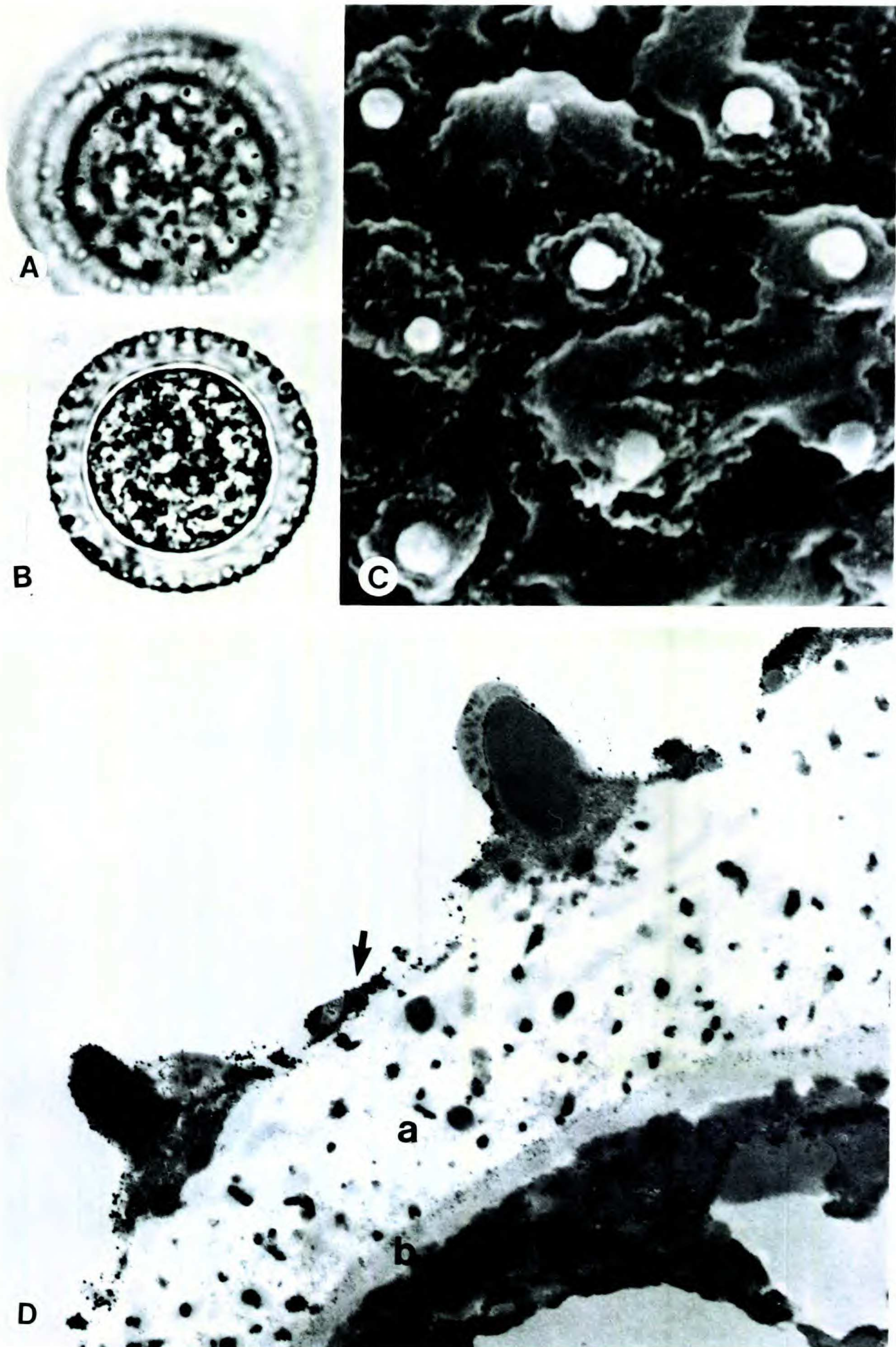


FIGURE 13. *Litsea glaucescens*.—A. Entire pollen grain showing spinules as white and dark dots.—B. The same in optical cross section. LM  $\times 1,000$ .—C. Part of exine showing spinules and their basal cushions. SEM  $\times 11,000$ .—D. Part of pollen wall showing an outer very thin, electron-dense exinous layer composed of scattered or irregularly clustered granular to globular elements (arrow). Intine distinctly differentiated into an outer, thick stratum inlaid with channels and vacuoles filled with osmiophilic material (a) and an inner thin, denser, homogeneous layer (b). TEM  $\times 20,000$ .



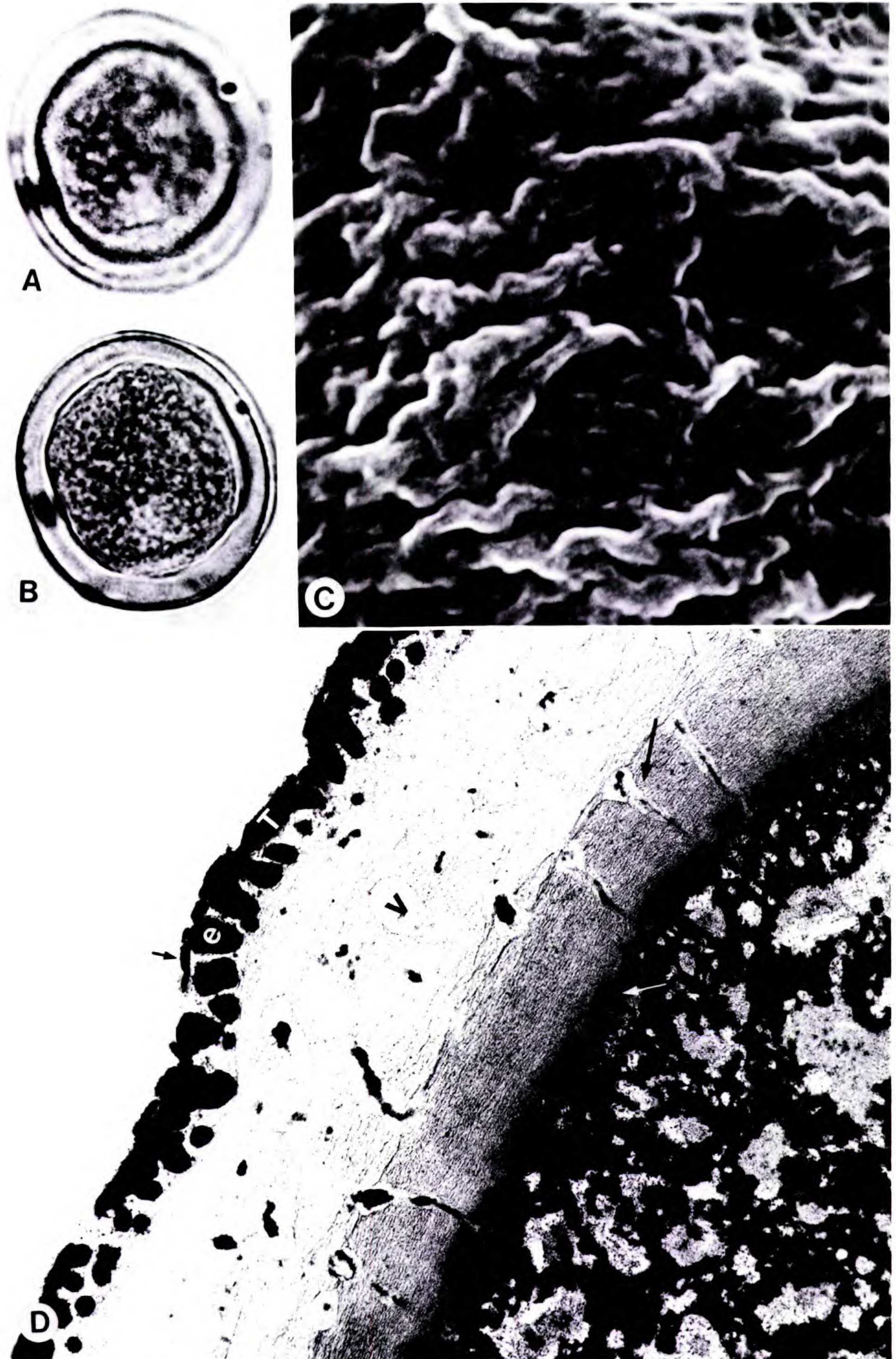


FIGURE 14. *Cryptocarya aschersoniana*.—A. Entire pollen grain showing the smooth exinous surface.—B. The same in optical cross section. LM  $\times 1,000$ .—C. Part of exine showing the smooth and wrinkled surface. SEM  $\times 11,000$ .—D. Part of pollen wall showing a thin, electron-dense layer consisting of tectum (T), supported by clavatelike to globular elements (e), and covered by a thin coating of compact material (arrow). The subtending intinous layer distinguished into an outer thick, fibrillar layer inlaid with vacuoles (v), followed by

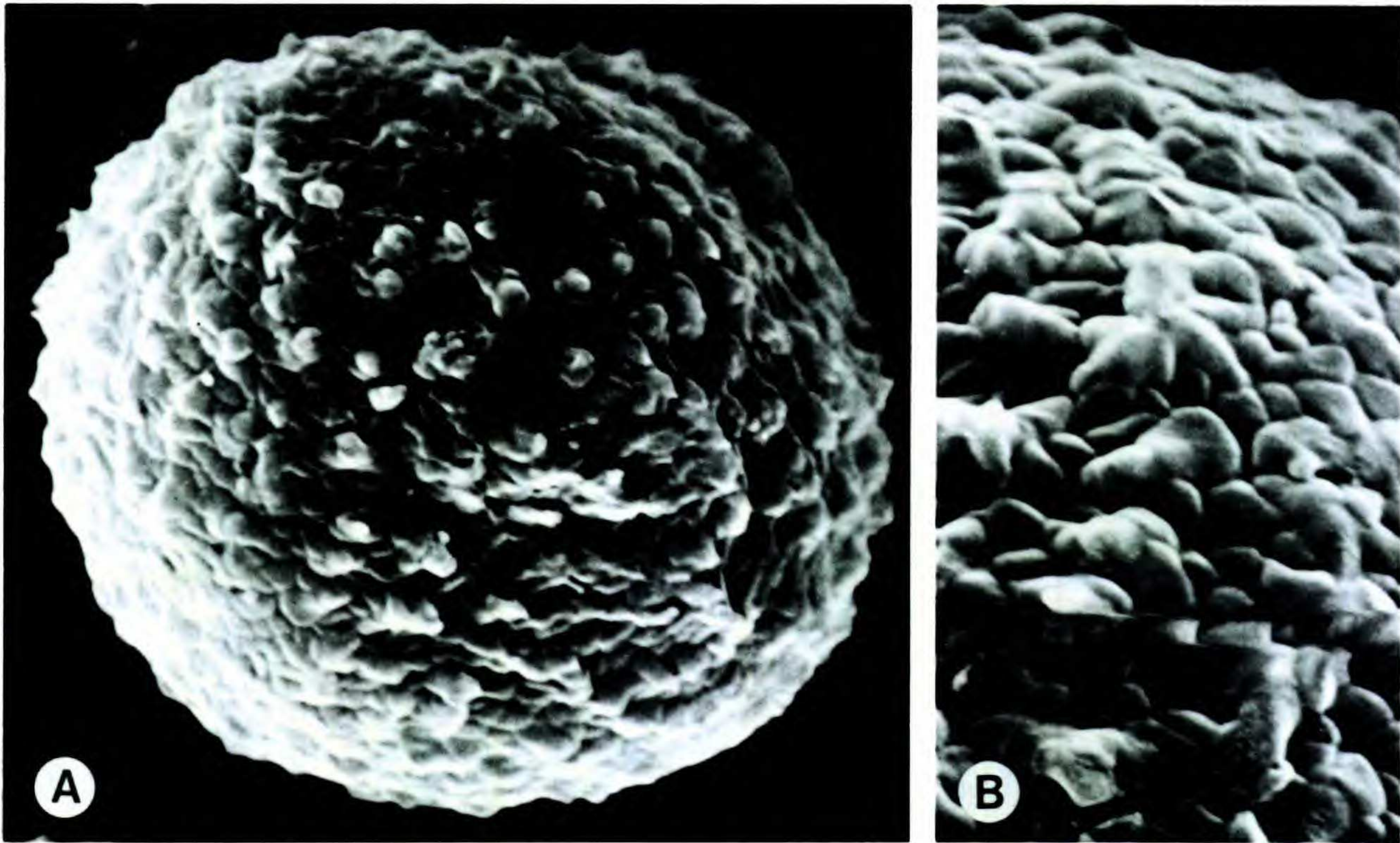


FIGURE 15. *Cassytha filiformis*.—A. Entire pollen grain showing uneven exinous surface beset with spinuloid processes. SEM  $\times 5,200$ .—B. Part of the same at a higher magnification. SEM  $\times 10,000$ .

grains in *Umbellularia californica* (not confirmed by the present investigation) and acolpate grains in *Laurus nobilis* (not included in the present study). Also Markgraf & D'Antoni (1978) described the pollen grains of *Nectandra angustifolia* as tricolpate, prolate spheroidal (not included in the present study).

The pollen grains of this family are considered to be "delicate" since they disintegrate readily or come out in a more or less shriveled and wrinkled condition after acetolysis. They are tenui-exinous and, as TEM observation shows, entirely ectexinous. The exine is provided with spinules or spinuloid projections, or rarely the exine is smooth as in *Cryptocarya aschersoniana* (Heusser, 1971, described the exine of *Cryptocarya alba* as foveolate). The intine represents the dominant, massive layer of the pollen wall.

Out of the 80 taxa investigated, the largest pollen grains are those of *Beilschmiedia miersii*, *Cryptocarya aschersoniana*, *Ocotea calophylla*, *O. spixiana*, *Persea amer-*

*icana*, *P. caerulea*, *P. fulva*, and others (over  $30\ \mu\text{m}$  in diameter); while the smallest belong to *Aniba burchellii*, *Endlicheria glomerata*, *Nectandra purpurea*, *Ocotea cernua*, and *Persea veraguasensis* (under  $20\ \mu\text{m}$  in diameter). In the remaining taxa the diameters are  $20\text{--}30\ \mu\text{m}$ . The grains are usually monomorphic; however, dimorphic grains occur in *Persea caerulea* and *P. schiedeana*.

Some species of *Persea* have dimorphic spinules. Because *Persea* shows various stages of reduction of the number of fertile stamens and/or anther cells (from the normal pattern of nine four-celled stamens to six four-celled and three two-celled or six four-celled stamens and three staminodia or nine two-celled stamens; Kopp, 1966), it would be worthwhile to investigate whether in species with dimorphic pollen grains each stamen has only one kind of pollen grain and inner and outer stamens have different pollen grains or whether each stamen possesses both kinds of pollen grains.

←  
an electron-dense, structurally compact, fibrillar stratum inlaid with narrow, conical channels (arrow); the innermost layer denser than the other layers and likewise inlaid with channels (white arrow). TEM  $\times 20,000$ .

TABLE 4. Pollen-morphological data for Lauraceae. Five main pollen characters are compared: (1) diameter of pollen grains; (2) exine thickness; (3) intine thickness; (4) length of spinules; and (5) maximum and minimum number of spinules.

	Dia- meter ( $\mu\text{m}$ )	Exine ( $\mu\text{m}$ )	Intine ( $\mu\text{m}$ )	Spinules ( $\mu\text{m}$ )	Maximum	Minimum	Remarks
Subfamily Lauroideae							
Tribe Perseeae							
Subtribe Perseineae							
<i>Persea</i>							
<i>P. americana</i>	30-36	0.5	4	< 0.5	1,174	815	spinules dimorphic, pointed and blunt, intermingled, 2 $\mu\text{m}$ apart
<i>P. caerulea</i>	33-39	1	3	0.5	661	612	pollen grains dimorphic (a) with monomorphic spinules (b) with dimorphic spinules; spinules small, thick, blunt or small, thin and pointed, 3 $\mu\text{m}$ apart
<i>P. fulva</i>	29-44	1	3	0.5	779	338	spinules in places dimorphic, 3 $\mu\text{m}$ apart; in places crowded, 1 $\mu\text{m}$ apart
<i>P. mutisii</i>	30-41	1	4	< 0.5	> 1,000	—	spinules dimorphic, pointed and blunt, intermingled, 1 $\mu\text{m}$ apart
<i>P. schiedeana</i>	31-36	1.5	3	< 1	4,700	3,485	pollen grains dimorphic (a) spinules monomorphic (b) spinules dimorphic, pointed and blunt intermingled, 1 $\mu\text{m}$ apart
<i>P. veraguasensis</i>	14-17	1	2	0.5	4,192	2,843	spinules 0.5 $\mu\text{m}$ apart
<i>Phoebe</i>							
<i>P. costaricana</i>	22-26	< 1	< 2	< 1	650	425	spinules 2 $\mu\text{m}$ apart
<i>P. hammeliana</i>	24-28	1	< 2	< 1	670	535	spinules 2 $\mu\text{m}$ apart
<i>P. helicterifolia</i>	24-27	2	3	< 2	660	521	spinules 2 $\mu\text{m}$ apart
<i>P. mexicana</i>	21-24	1	2	< 1	2,088	1,599	spinules 1 $\mu\text{m}$ apart
<i>P. porphyria</i>	22-28	1	3	< 1	2,843	1,755	spinules 1 $\mu\text{m}$ apart
<i>P. smithii</i>	30-33	1	3	< 1	631/987	521/815	spinules 2-2.5 $\mu\text{m}$ apart, occasionally paired in places
<i>Caryodaphnopsis</i>							
<i>C. fosteri</i>	27-33	0.5	2	1.5	661	437	spinules 2-3 $\mu\text{m}$ apart
Subtribe Beilschmiedineae							
<i>Beilschmiedia</i>							
<i>B. miersii</i>	28-38	2	2.5	1.5	710	580	spinules 2-3 $\mu\text{m}$ apart
<i>B. pendula</i>	23-29	1	5	1	762	479	spinules 2 $\mu\text{m}$ apart; in places 0.5 $\mu\text{m}$ apart
<i>Mezilaurus</i>							
<i>M. navatum</i>	22-26	1	2	< 0.5	650	425	spinules 2 $\mu\text{m}$ apart

TABLE 4. Continued.

	Dia- meter ( $\mu\text{m}$ )	Exine ( $\mu\text{m}$ )	Intine ( $\mu\text{m}$ )	Spinules ( $\mu\text{m}$ )	Maximum	Minimum	Remarks
Tribe Cinnamomeae							
Subtribe Cinnamomineae							
<i>Ocotea</i>							
<i>O. calophylla</i>	31-39	1	3	1	612	386	spinules 3 $\mu\text{m}$ apart
<i>O. cernua</i>	17-19	1	2	< 0.5	1,309	1,047	spinules 1 $\mu\text{m}$ apart
<i>O. corymbosa</i>	22-25	1	2	1	2,266	1,755	spinules 1 $\mu\text{m}$ apart
<i>O. cuprea</i>	24-27	1	3	1	660	521	spinules 2 $\mu\text{m}$ apart, frequently crowded on insulae
<i>O. dendrodaphne</i>	26-29	1.5	2.5	1	762	612	spinules 2 $\mu\text{m}$ apart
<i>O. ensifolia</i>	26-28	1.5	2	1.5	928/412	612/271	spinules 2-3 $\mu\text{m}$ apart
<i>O. guianensis</i>	20-26	1.5	2	1	2,451/612	1,450/362	spinules 1-2 $\mu\text{m}$ apart
<i>O. ira</i>	23-28	1	3	< 0.5	2,843	1,918	spinules 1 $\mu\text{m}$ apart, transparent, weak colpulike or porelike areas seen in a few grains
<i>O. kuhlmannii</i>	24	1.5	2	1	612	521	spinules 2 $\mu\text{m}$ apart
<i>O. oblonga</i>	20-24	1	2	< 0.5	521	362	spinules 2 $\mu\text{m}$ apart
<i>O. puberula</i>	24-27	1.5	2.5	1	292	231	spinules 3 $\mu\text{m}$ apart
<i>O. pulchella</i>	27-31	2	1.5	1	557	422	spinules 2.5 $\mu\text{m}$ apart
<i>O. skutchii</i>	24-27	1	4	< 0.5	661	521	spinules 2 $\mu\text{m}$ apart
<i>O. spixiana</i>	34-39	2	3	2	344	261	spinules 4 $\mu\text{m}$ apart
<i>O. tonduzii</i>	25-27	1	2	1	2,643	2,266	spinules 1 $\mu\text{m}$ apart
<i>O. veraguensis</i>	18-20	1	2	< 0.5	> 1,000	—	spinules 1 $\mu\text{m}$ apart
<i>O. villosa</i>	27-29	2.5	5	2	762	666	spinules 2 $\mu\text{m}$ apart
<i>O. whitei</i>	30-33	1	3	< 0.5	3,949	3,264	spinules 1 $\mu\text{m}$ apart
<i>Nectandra</i>							
<i>N. acutifolia</i>	22-24	0.5	1.5	< 0.5	521	438	spinules 2 $\mu\text{m}$ apart
<i>N. ambigens</i>	28-33	0.5	2	1.5	710	437	spinules 2-3 $\mu\text{m}$ apart
<i>N. baccans</i>	24-29	1	2.5	< 1	762	521	spinules 2 $\mu\text{m}$ apart
<i>N. cissiflora</i>	18-20	0.5	3	< 0.5	1,309	1,309	spinules 1 $\mu\text{m}$ apart
<i>N. coriacea</i>	19-25	1	2	0.5	251	144	spinules 1.5-3 $\mu\text{m}$ apart
<i>N. cuspidata</i>	26-29	1	2	< 0.5	762	612	spinules 2 $\mu\text{m}$ apart
<i>N. falcifolia</i>	26-29	0.5	2.5	0.5	338/190	271/152	spinules 3-4 $\mu\text{m}$ apart, in places crowded; dimorphic?
<i>N. gardneri</i>	28-33	1	3	1	986	710	spinules 2 $\mu\text{m}$ apart
<i>N. gentlei</i>	22-27	1	4	0.5	2,643	1,755	spinules 1 $\mu\text{m}$ apart

TABLE 4. Continued.

	Dia- meter ( $\mu\text{m}$ )	Exine ( $\mu\text{m}$ )	Intine ( $\mu\text{m}$ )	Spinules ( $\mu\text{m}$ )	Maximum	Minimum	Remarks
<i>N. globosa</i>	21-24	0.5	2.5	1	521	399	spinules 2 $\mu\text{m}$ apart
<i>N. grandiflora</i>	25-27	1	3.5	1	293	251	spinules 3 $\mu\text{m}$ apart
<i>N. lanceolata</i>	26-31	1.5	2.5	1	871	612	spinules 2 $\mu\text{m}$ apart
<i>N. loeseneri</i>	19-23	1	2	0.5	1,918	1,309	spinules 1 $\mu\text{m}$ apart
<i>N. martinicensis</i>	19-22	1	2	1	438	326	spinules 2 $\mu\text{m}$ apart
<i>N. membranacea</i>	20-25	1	2	< 0.5	2,266	1,450	spinules 1 $\mu\text{m}$ apart
<i>N. perdubia</i>	19-24	0.5	2	1	928	581	spinules 1.5 $\mu\text{m}$ apart
<i>N. purpurea</i>	18-19	1	2	< 0.5	1,309	1,174	spinules 1 $\mu\text{m}$ apart
<i>N. reticulata</i>	27-30	1	2	1	815	660	spinules 2 $\mu\text{m}$ apart
<i>N. salicifolia</i>	22-27	1	2	1	660	438	spinules 2 $\mu\text{m}$ apart
<i>N. salicina</i>	23-26	1	3	< 0.5	612	479	spinules 2 $\mu\text{m}$ apart
<i>Pleurothyrium</i>							
<i>P. densiflorum</i>	21-24	0.5	1.5	< 0.5	2,088	1,599	spinules 1 $\mu\text{m}$ apart
<i>P. zulianense</i>	22-24	0.5	1.5	< 0.5	2,088	1,755	spinules 1 $\mu\text{m}$ apart
<i>P. sp.</i>	28-30	0.5	1.5	1	815	710	spinules 2 $\mu\text{m}$ apart
<i>Rhodostemonodaphne</i>							
<i>R. grandis</i>	21-23	0.5	2.5	< 0.5	1,918	1,599	spinules 1 $\mu\text{m}$ apart; $\pm$ vestigial
<i>R. kunthiana</i>	21-24	1	1	< 0.5	2,088/521	1,599/399	spinules 1-2 $\mu\text{m}$ apart
<i>Umbellularia</i>							
<i>U. californica</i>	31-36	3.5	2.5	1	521	386	spinules 3 $\mu\text{m}$ apart
Subtribe Anibineae							
<i>Aiouea</i>							
<i>A. costaricensis</i>	22-29	1	3	< 0.5	762/338	438/194	spinules 2-3 $\mu\text{m}$ apart; porelike transparent areas devoid of spinules discernible
<i>A. laevis</i>	19-21	0.5	1.5	< 0.5	1,599	1,309	spinules 1 $\mu\text{m}$ apart
<i>A. trinervis</i>	20-23	1	3	< 0.5	479	361	spinules 2 $\mu\text{m}$ apart
<i>Aniba</i>							
<i>A. burchellii</i>	18-20	0.5	1.5	< 0.5	1,450	1,174	spinules 1 $\mu\text{m}$ apart
<i>A. canelilla</i>	22-27	0.5	1.5	< 0.5	2,643	1,755	spinules 1 $\mu\text{m}$ apart
<i>A. firmula</i>	20-23	0.5	1.5	< 0.5	1,918	1,450	spinules 1 $\mu\text{m}$ apart; in a few pollen grains distinct 2-3 porelike or irregular openings seen
<i>A. riparia</i> $\times$ <i>kappleri</i>	16-19	0.5	2	< 0.5	5,237	3,714	spinules 0.5 $\mu\text{m}$ apart

TABLE 4. Continued.

	Dia- meter ( $\mu\text{m}$ )	Exine ( $\mu\text{m}$ )	Intine ( $\mu\text{m}$ )	Spinules ( $\mu\text{m}$ )	Maximum	Minimum	Remarks
<i>Endlicheria</i>							
<i>E. endlicheriopsis</i>	17-21	0.5	2	< 0.5	1,599	1,047	spinules 1 $\mu\text{m}$ apart
<i>E. glomerata</i>	15-19	0.5	2.5	0.5	1,309	815	spinules 1 $\mu\text{m}$ apart
<i>E. paniculata</i> subsp. <i>poeppigii</i>	17-22	0.5	2	< 0.5	7,022	4,192	spinules 0.5 $\mu\text{m}$ apart
<i>E. sericea</i>	24-27	1	2	1	660	521	spinules 2 $\mu\text{m}$ apart
<i>E. tessmannii</i>	16-20	0.5	1.5	< 0.5	1,450	928	spinules 1 $\mu\text{m}$ apart
<i>E. verticillata</i>	20-25	1	1	< 0.5	2,266	1,450	spinules 1 $\mu\text{m}$ apart
<i>Licaria</i>							
<i>L. armeniaca</i>	27-33	1	3	< 0.5	3,949	2,643	spinules 1 $\mu\text{m}$ apart
<i>L. capitata</i>	20-25	1	2.5	< 0.5	> 1,000	565	spinules 1-2 $\mu\text{m}$ apart
<i>L. peckii</i>	23-25	0.5	3.5	< 0.5	2,266/1,754	566/479	spinules 1-2 $\mu\text{m}$ apart
<i>L. triandra</i>	17-23	0.5	1.5	< 0.5	1,918	1,047	spinules 1 $\mu\text{m}$ apart
<i>Kubitzkia</i>							
<i>K. mezii</i>	24-27	< 1	> 3	0.5	661	521	spinules 2 $\mu\text{m}$ apart
Tribe Litseeae							
Subtribe Litseineae							
<i>Litsea</i>							
<i>L. glaucescens</i>	27-35	1	4	< 1	493	293	spinules 3 $\mu\text{m}$ apart
Tribe Cryptocaryeae							
Subtribe Cryptocaryineae							
<i>Cryptocarya</i>							
<i>C. aschersoniana</i>	30-33	0.5	4	absent	—	—	exine smooth or wrinkled, its surface appearing interrupted
Subfamily Cassythoideae							
<i>Cassytha</i>							
<i>C. filiformis</i>	22-28	1	4	0.5	—	—	exine surface beset with densely spaced, minute excrescences

The exine ornamentation in all the taxa (except *Cryptocarya*) consists of solid, apparently simple spinules or as in *Nectandra reticulata*, *Ocotea cuprea*, *Persea americana*, *Phoebe porphyria*, and others, "wick-like" i.e., made up of twisted strands. They are pointed or blunt, uniformly spread over the surface or rarely, in some portions of a grain, in groups; the spinules are sometimes crowded as in *Nectandra ambigens* to give a rosettelike appearance, or they occur in pairs. Similar wicklike spinules have been reported in many groups, e.g., Euphorbiaceae (Thanikaimoni et al., 1984), Linaceae (Punt & den Breejen, 1981), Monimiaceae (Walker & Doyle, 1975) and Plumbaginaceae (Nowicke & Skvarla, 1977).

The density and morphology of spinules differs in different species. Thus the highest number of spinules per grain is met with in *Persea* and *Licaria*, and the lowest in *Beilschmiedia*, *Caryodaphnopsis*, and *Litsea*. Further, the size of the pollen grains does not seem related to the number of spinules. Spinules are usually monomorphic; however, dimorphic spinules have been found in *Nectandra falcifolia*, *Persea caerulea*, and *P. fulva*. Spinules are usually broad at base. Their common characteristic feature is the presence of a conspicuous, circular, cushion-like base which invariably protrudes proximally; its surface is either smooth or studded with granular to globular elements. In *Ocotea cuprea* these cushionlike structures are relatively big and compactly arranged, thereby giving a more or less rounded insulaelike appearance to the exine.

The stratification of the sporoderm presents interesting features that at times are difficult to interpret. A strikingly similar type of stratified sporoderm has been reported in the Zingiberales and in certain monimiaceous genera. The fascinating aspect of the pollen wall is the extreme thinness of the exine and the thick, structurally complex intine.

The fine structure of the lauraceous genera investigated shows an electron-dense, extremely thin, coherent exine made up of granular, globular, or irregularly shaped elements

and of spinules. Only in *Persea fulva* (Fig. 1C), *Endlicheria serica* (Fig. 11A), and *Cryptocarya aschersoniana* (Fig. 14D) is there a clear indication of parts of well-defined tectum supported by a well-defined bacular layer. In *Umbellularia californica* the exine surface and spinules are covered by a distinct, superficial coating referred to as "fuzzy surface coating" by Rowley & Skvarla (1986); traces of this material are also discernible in *Aiouea trinervis*, *Ocotea puberula*, *Persea fulva*, and *Phoebe helicterifolia*.

The coherent nature of the thin exine, which is emphasized in the present study, has often been compared with exines of some members of the Zingiberales (Kress et al., 1978; Stone et al., 1979) and reported as incoherent or "exine-less." The incoherent nature of any exine, however thin, or the conception of an "exine-less" pollen wall, both from a morphological and functional point of view, has been convincingly argued and rejected by Hesse & Waha (1983).

The dominant stratified layer of the sporoderm is the intine. This thick layer is completely destroyed by acetolysis and, in keeping with common wisdom, has to be interpreted as intine. In this layer an outer channeled zone can be easily recognized and has been designated variably: "lacunes" after Le Thomas, 1980; "tubules" according to Sedgley, 1979; "onciform zone" by Rowley & Vasanthi, 1980; "Zwischenkörper" in Kress & Stone, 1982; or simply outer intine or intine 1. These channels, which are long and narrow and of varying length, are predominantly radially aligned and partly or completely filled with osmiophilic material. Thin partition walls as encountered in *Strelitzia reginae* (Musaceae) (Hesse & Waha, 1983) are absent. It is postulated that these channels may act as deposits for material involved in pollen germinating or incompatibility processes (Stone et al., 1979; Hesse & Kubitzki, 1983).

It is remarkable that the characteristic sporoderm stratification encountered in lauraceous genera, namely extremely thin exine and a thick, stratified, channeled intine, is

apparently limited to inaperturate pollen grains belonging to such disparate genera as *Canna*, *Heliconia*, *Hernandia*, and *Palmeria*.

Further, the massive channeled intinous zone mentioned above has been found also to resemble to a lesser extent that of the conifers (viz., *Larix europea*, Cupressineae, and Taxodineae) that Wodehouse (1932) noted and remarked as "one of the most remarkable examples of convergence I have yet encountered among pollen-grain forms."

The functional significance of the thickened intinous layers or onci frequently observed beneath apertures appears to be to act as storage areas for gametophytic incompatibility proteins (Heslop-Harrison, 1976).

#### TAXONOMY

There is uniformity of opinion among taxonomists that the family Lauraceae is rather old and probably derived from primitive members of the Monimiaceae of the *Hortonia*-type.

In Kostermans's (1957) classification, only a sequence of floral characters are adopted; not a chronological family tree, nor a paleontological succession, nor a phylogenetic trend has been envisaged, but similar genera are grouped.

Palynologically most of the relationships are justified, e.g., the genera *Persea* and *Phoebe* of the tribe Perseeae are satisfactorily included in the subtribe Perseineae, and thus separated from *Beilschmiedia* and *Mezilaurus* of the subtribe Beilschmiediineae. The pollen grains of *Persea* and *Phoebe* have the highest number of spinules per pollen grain, and their anthers are four-celled compared with *Beilschmiedia* and *Mezilaurus*, which have the lowest number of spinules and have two-celled anthers. The former two genera are easily separated from each other because the pollen grains of *Persea* are either dimorphic or if monomorphic, the spinules are dimorphic, whereas the pollen grains of *Phoebe* are wholly monomorphic. Among the Central American species of *Phoebe*, *P. mexicana* stands clearly apart due to its high number

of spinules. This pollen feature supports the recognition of *P. costaricana* as distinct from *P. mexicana*.

The genera *Beilschmiedia* and *Mezilaurus* can be separated by the difference in size of spinules and in the surface of the basal cushions and exine. Pollen-morphologically, *Mezilaurus* does not seem to be close to *Licaria*.

*Caryodaphnopsis*, although similar to *Persea* in floral and fruit characters, has pollen grains quite unlike those of *Persea* and *Phoebe*. On the other hand, the pollen grains are comparable to those of *Beilschmiedia*, and recognition of *Caryodaphnopsis* is supported by pollen morphology. Its position in Richter's (1981) classification seems to be more appropriate than in those of Kostermans (1957) and Hutchinson (1964).

Kostermans (1957) divided *Ocotea*, of the tribe Cinnamomeae, subtribe Cinnamomiinae, into three subgenera: *Ocotea*, *Nectandra* and *Pleurothyrium*. His contention that macromorphological differences, such as in the position of the anther cells, size and shape of the staminal glands, and cupule shape, are not big enough to maintain them as distinct genera does not improve the classification. Pollen-morphologically there are enough differences to recognize them as distinct genera. Pollen grains of *Ocotea* and *Pleurothyrium* are apparently very similar, including the organization of spinules, which suggest close relationship. However, the characters that distinguish them are pollen size and ultrastructural details of sporoderm. Pollen grains of *Nectandra* are quite distinct with respect to exine surface and to sporoderm details. There seems enough micro- and macromorphological characters to maintain these as three distinct genera. The transfer of the two species *Nectandra grandis* (Fig. 6D) and *N. kunthiana* to the new genus *Rhodostemonodaphne* (Rohwer, 1986) seems justified, as the pollen grains are quite different from those of the other species investigated. The spinules in both species appear vestigial without the usual twisted strands easily discernible in other species.



The monotypic genus *Umbellularia* is considered to be related to *Litsea*. Pollen-morphologically such a relationship seems to exist as the pollen grains of the two genera are more or less of the same size, the number of spinules per pollen grain is more or less the same, and the ultrastructural details of the pollen wall are very similar.

Subtribe Anibineae of tribe Cinnamomeae is represented by seven genera, of which the pollen grains of five, *Aiouea*, *Aniba*, *Endlicheria*, *Licaria* and *Kubitzkia* (*Systemonodaphne* sensu Mez), have been investigated. These five genera are rather closely related, and taxonomic problems still remain unsolved in this group. *Aiouea*, recently revised by Renner (1982), appears to include species independently derived from four-celled ancestors. Some Central American *Aiouea* species are morphologically very similar to sympatric *Ocotea* species (van der Werff, 1987) and are much less similar to the Guyanan-Brazilian species group which includes the type species. The observation that *Ocotea ira* and *Aiouea costaricensis* both possess porelike, transparent areas devoid of spinules on the pollen wall (otherwise a very rare character in Lauraceae) strengthens the theory that *Aiouea costaricensis* is more closely related to sympatric *Ocotea* species of the *O. insularis* group (as defined by Rohwer, 1986) than to the S. American *Aiouea* species, and that *Aiouea* is a polyphyletic genus. Kubitzki (1982) considered *Aniba* and *Licaria* closely related but had no hesitation in maintaining them as separate genera, a point of view we share. MacBride's (1938) suggestion to treat *Licaria*, *Kubitzkia*, and *Endlicheria* (the only dioecious genus in this group) as subgenera of *Aniba* has never gained acceptance. *Kubitzkia* is probably closely related to *Licaria*, but is easily separated by the number of fertile stamens.

Pollen morphology also supports the interrelationship of the above genera, and at the same time distinguishes them from one another. All genera have pollen grains of more or less the same size and exhibit the highest number of spinules (excluding *Kubitzkia*) per pollen grain. The highest number of spinules

is found in *Licaria*. There is a gradual decrease from *Endlicheria* to *Aniba* to *Aiouea*. *Kubitzkia*, with a much lower number of spinules per pollen grain (661/521), seems to be a misfit in this subtribe, and pollen morphology fails to support its taxonomic relationship with *Licaria*. Better placement would be in the vicinity of *Beilschmiedia* as classified by Hutchinson (1964).

In *Aiouea* the basal cushion of spinules is more or less smooth or in places surrounded by a ring of partially fused processes. In *Aniba* the basal cushions are not very pronounced, and the general surface of the exine is studded with granular processes. In *Endlicheria* densely spaced processes surround and hide the basal cushion of spinules. In *Licaria* the basal cushions are smooth and surrounded by a ring of densely spaced, partially fused processes of varying size and shape, and the general surface of exine is studded with densely spaced granular processes. In *Kubitzkia* the basal cushion of spinules is prominent and surrounded by a ring of densely spaced, partially fused processes of varying size and shape; the general surface of exine is studded with densely spaced, minute processes. Another group of pollen morphological features that distinguish these genera (except *Kubitzkia*, not investigated by TEM) are the ultrastructural details of the sporoderm.

In the classification proposed by Kostermans (1957), *Litsea* is included in subtribe Litseineae of tribe Litseeae. It is closely related to *Umbellularia*, and pollen morphology justifies this relationship. Pollen morphology would thus support the transfer of *Umbellularia* to subtribe Litseineae, corresponding with the classification of Hutchinson (1964) and Richter (1981).

*Cryptocarya* of tribe Cryptocaryeae, subtribe Cryptocaryineae, is considered isolated among the neotropical genera. Its isolated position is very well reflected in its pollen grains. Its pollen grains are quite different from those of the other genera investigated. The exine surface is devoid of spinules and spinuloid excrescences, instead it appears smooth and wrinkled. The inclusion of this genus by Richter (1981) is his Group I, along

with *Beilschmiedia* and *Caryodaphnopsis*, is not supported pollen-morphologically.

*Cassytha*, of subfamily Cassythoideae, is a parasitic or partially autotrophic twiner. Because of its aberrant habit and ecology, it has often been treated as a separate family, Cassythaceae, but in floral characters it resembles Lauraceae and approaches *Cryptocarya*. The pollen grains of *Cassytha* are characteristic and unlike those of the other genera except *Cryptocarya*, which it resembles in the wrinkled exine surface but from which it differs by the presence of minute, scattered, irregular projections or low warts.

From the above account, pollen characters have been found useful in elucidating relationships of many genera but inadequate to clarify the positions of others. However, in the absence of any clear characters, it is important to assess critically each line of evidence and this we have attempted to do for the palynological data.

The treatment of Laurales in both classical and modern systems of classification is as a considerably old order. Hutchinson (1964) placed Laurales in his Lignoseae, this consisting of woody families. Engler (1936), however, did not consider the order as so primitive—in his view the amentiferous plants were the most ancient dicotyledons. Cronquist (1968) regarded the members of Laurales as rather primitive and placed them in the most primitive order Magnoliales. Takhtajan (1969), while formulating his system, took into account the importance of pollen morphology and considered the Magnoliales as the most primitive order; he accepted Laurales as near Magnoliales but slightly more advanced.

The inaperturate type of pollen grains of Lauraceae are also encountered in some families of Laurales, such as Amborellaceae, Gomortegaceae, Gyrocarpaceae, and Hernandiaceae and in *Sarcandra* (Chloranthaceae), *Hortonia*, *Levieria*, *Peumus*, and *Tambourissa* (Monimiaceae). The rest of lauralean families exhibit apertures that are monosulcate or disulcate or diporate. It is believed that the inaperturate condition is palynologically more advanced than a monosulcate con-

dition from which the former has been derived; Doyle (1969) postulated such derivation on the basis of the Cretaceous pollen record.

Kostermans (1957) postulated a development within the Lauraceae from genera with a very shallow floral tube, where the fruit is not subtended by a cupule (tribe Perseeae), through genera with a deeper floral tube, where the fruit at maturity is subtended by a cupule up to one-third the size of the fruit (tribe Cinnamomeae) and genera with a deep floral tube that fully encloses the fruit (tribe Cryptocaryeae). If the pollen-morphological data are interpreted in relation to this view, *Persea* could be regarded as the most primitive genus because of the large number of spinules; and if the reduction of the number of spinules is interpreted as an advanced trait, *Cryptocarya*, because of the total absence of spinules, would stand out as advanced. Thus these two genera would represent the two extremes, and the remaining genera, because of the intergrading characteristics (size of pollen grains and number of spinules), would fall in between but not necessarily in a phylogenetic sequence. *Cassytha* is the only herbaceous genus that is distinct from the rest of the genera because of its habit. The pollen grains exhibit spinules reduced into minute excrescences, and this suggests a major evolutionary trend. Pollen morphology might provide additional evidence to support separating *Cassytha* into a subfamily of its own.

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- LIST OF SPECIES INVESTIGATED
- Aiouea* Aubl.  
*A. costaricensis* (Mez) Kosterm.—Costa Rica, *Hartshorn* 1121.  
*A. laevis* (Mart.) Kosterm.—Venezuela, *Bernardi* 7937.  
*A. trinervis* Meissn.—Brazil, *Mori* 16711.
- Aniba* Aubl.  
*A. burchellii* Kosterm.—Brazil, *Heringer & Eiten* 15154.  
*A. canelilla* (Kunth) Mez—Brazil, *Heringer et al.* 16021.  
*A. firmula* (Nees & Mart.) Mez—Brazil, *Cult. Bot. Gardn. Rio de Janeiro* 110302.  
*A. riparia* × *A. kappleri*—Venezuela, *L. Marcano Berti* 334.
- Beilschmiedia* Nees  
*B. miersii* (Gay) Kosterm.—Chile, *Zöllner* 11607.  
*B. pendula* (Sw.) Benth.—Panama, *Croat* 12928.
- Caryodaphnopsis* Airy Shaw  
*C. fosteri* v. d. Werff—Peru, *Foster* 9585.
- Cassytha* L.  
*C. filiformis* L.—Venezuela, *Liesner & Gonzalez* 5783.
- Cryptocarya* R. Br.  
*C. aschersoniana* Mez—Brazil, *Hoehne s.n.*
- Endlicheria* Nees  
*E. endlicheriopsis* (Mez) Kosterm.—Maguire 24898a.  
*E. glomerata* Mez—Brazil, *Heringer & Eiten* 15154.  
*E. paniculata* (Spreng.) MacBr. subsp. *poepigii* (Kosterm.) Koch, ined.—Peru, *Schunke* 2924.  
*E. sericea* Nees—Brazil, *Ratter et al.* 1278.  
*E. tessmannii* O. C. Schmidt—Peru, *Croat* 20771.  
*E. verticillata* Mez—Peru, *Woytkowski* 6304.
- Kubitzkia* v. d. Werff  
*K. mezii* (Kosterm.) v. d. Werff—Brazil, *Pires et al.* 50919 (NY); Surinam, *Irwin* 55719.
- Licaria* Aubl.  
*L. armeniaca* (Nees) Kosterm.—Peru, *Revilla et al.* 2571.  
*L. capitata* (Schlecht. & Cham.) Kosterm.—Guatemala, *Lundell* 15769.  
*L. peckii* (I. M. Johnston) Kosterm.—Belize, *Proctor* 36035.
- L. triandra* (Sw.) Kosterm.—Venezuela, *Steyermark et al.* 122775.
- Litsea* Lam.  
*L. glaucescens* Kunth—Mexico, *Breedlove* 33 753.
- Mezilaurus* Taubert  
*M. navalium* (Allemao) Taubert—Brazil, *Glaziou* 1212.
- Nectandra* Roland. ex Rottb.  
*N. acutifolia* (Ruiz & Pavon) Mez—Ecuador, *Mexia* 8465.  
*N. ambigens* (Blake) Allen—Mexico, *Wendt et al.* 3190.  
*N. baccans* (Meissn.) Mez—Venezuela, *Aristeguieta* 7281.  
*N.?* *cissiflora* Nees—Bolivia, *Krukoff* 10890.  
*N. coriacea* (Sw.) Griseb.—Mexico, *Breedlove* 24564.  
*N. cuspidata* Nees—Brazil, *Irwin et al.* 21038.  
*N. falcifolia* (Nees) Castigl.—Argentina, *Krapovickas & Irigoyen* 18390.  
*N. gardneri* Meissn.—Brazil, *Irwin et al.* 16647.  
*N. gentlei* Lundell—Panama, *Mori & Kallunki* 2996.  
*N. globosa* (Aubl.) Mez—Panama, *Croat* 7343.  
*N. grandiflora* Nees—Brazil, *Hatschbach* 32569.  
*N. lanceolata* Nees—Argentina, *Schwarz* 5103.  
*N. loeseneri* Mez—Mexico, *Brigada Vazquez* 1575.  
*N. martinicensis* Mez—Costa Rica, *Hartshorn* 1226; Venezuela, *Liesner et al.* 7927.  
*N. membranacea* (Sw.) Griseb.—Costa Rica, *Hartshorn* 1753.  
*N. perdubia* Lundell—Mexico, *Hinton* 13918.  
*N. purpurea* (Ruiz & Pavon) Mez—Panama, *Croat* 7834.  
*N. reticulata* (Ruiz & Pavon) Mez—Mexico, *Dorantes* 4176.  
*N. salicifolia* (Kunth) Nees—Guatemala, *R. Tun Ortiz* 821.  
*N. salicina* Allen—Costa Rica, *Koptur SK-103.*
- Ocotea* Aubl.  
*O. calophylla* Mez—Colombia, *García-Barriga* 20740.  
*O. cernua* (Nees) Mez—Belize, *Proctor* 36013.  
*O. corymbosa* (Meissn.) Mez—Brazil, *Smith et al.* 14596.  
*O. cuprea* Mez—Peru, *Rimachi* 4499.  
*O. dendrodaphne* Mez—Costa Rica, *Burch* 4589.  
*O. ensifolia* Mez—Brazil, *Eiten* 10923.  
*O. guianensis* Aubl.—Venezuela, *Steyermark* 117621.  
*O. ira* Mez & Pitt.—Panama, *Lao & Gentry* 548.  
*O. kuhlmannii* Vattimo—Brazil, *Handro s.n.*  
*O. oblonga* (Meissn.) Mez—Panama, *Croat* 16515.  
*O. puberula* Nees—Panama, *Nee & Gentry* 8683.  
*O. pulchella* Mart.—Brazil, *Hatschbach* 20405.  
*O. skutchii* Allen—Panama, *Croat* 9780.  
*O. spixiana* (Nees) Mez—Brazil, *Chagas* 332.  
*O. tonduzii* Standl.—Costa Rica, *Haber* 191.  
*O. veraguensis* (Meissn.) Mez—Mexico, *Brigada Dorantes* 2881.  
*O. villosa* Kosterm.—Brazil, *Ramalho* 1863-RB208640.  
*O. whitei* Woodson—Panama, *Mori & Kallunki* 5625.
- Persea* Mill.  
*P. americana* Miller—Mexico, *Q. Valdivia* 176.  
*P. caerulea* (Ruiz & Pavon) Mez—Venezuela, *Steyermark* 104771.  
*P. fulva* Kopp—Brazil, *Irwin et al.* 30301.  
*P. mutisii* Kunth—Venezuela, *Luteyn & Lebrón-Luteyn* 6051.

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- P. schiedeana* Nees—Panama, *Hammel et al.* 6966.  
*P. veraguasensis* Seem.—Panama, *Tyson* 6689.
- Phoebe* Nees
- P. costaricana* Mez & Pittier—Panama, *v. d. Werff* 7315.  
*P. hammeliana* Burger, ined.—Costa Rica, *Hammel* 14091.  
*P. helicterifolia* (Meissn.) Mez—Mexico, *Breedlove* 34800.  
*P. mexicana* Meissn.—Panama, *Croat* 14674.  
*P. porphyria* (Griseb.) Mez—Argentina, *Venturi* 7554.  
*P. smithii* Allen—Costa Rica, *Hartshorn* 2130.
- Rhodostemonodaphne* Rohwer & Kubitzki
- R. grandis* (Mez) Rohwer—Venezuela, *Blanci* 278.  
*R. kunthiana* (Nees) Rohwer—Peru, *Croat* 19790.
- Pleurothyrium* Nees
- P. densiflorum* A. C. Smith—Peru, *Gentry & Reville* 16627.  
*P. zulianense* Lasser—Venezuela, *de Bruyn* 1422.  
*P. sp.*—Peru, *Kayap* 145.
- Umbellularia* Nutt.
- U. californica* (Hook. & Arn.) Nutt.—U.S.A., Cult. California, Berkeley, *Axelrod s.n.*